This is a digital copy of a book that was preserved for generations on library shelves before it was carefully scanned by Google as part of a project to make the world's books discoverable online.

It has survived long enough for the copyright to expire and the book to enter the public domain. A public domain book is one that was never subject to copyright or whose legal copyright term has expired. Whether a book is in the public domain may vary country to country. Public domain books are our gateways to the past, representing a wealth of history, culture and knowledge that's often difficult to discover.

Marks, notations and other marginalia present in the original volume will appear in this file - a reminder of this book's long journey from the publisher to a library and finally to you.

## Usage guidelines

Google is proud to partner with libraries to digitize public domain materials and make them widely accessible. Public domain books belong to the public and we are merely their custodians. Nevertheless, this work is expensive, so in order to keep providing this resource, we have taken steps to prevent abuse by commercial parties, including placing technical restrictions on automated querying.

We also ask that you:

+ *Make non-commercial use of the files* We designed Google Book Search for use by individuals, and we request that you use these files for personal, non-commercial purposes.

+ *Refrain from automated querying* Do not send automated queries of any sort to Google's system: If you are conducting research on machine translation, optical character recognition or other areas where access to a large amount of text is helpful, please contact us. We encourage the use of public domain materials for these purposes and may be able to help.

+ *Maintain attribution* The Google "watermark" you see on each file is essential for informing people about this project and helping them find additional materials through Google Book Search. Please do not remove it.

+ *Keep it legal* Whatever your use, remember that you are responsible for ensuring that what you are doing is legal. Do not assume that just because we believe a book is in the public domain for users in the United States, that the work is also in the public domain for users in other countries. Whether a book is still in copyright varies from country to country, and we can't offer guidance on whether any specific use of any specific book is allowed. Please do not assume that a book's appearance in Google Book Search means it can be used in any manner anywhere in the world. Copyright infringement liability can be quite severe.

## About Google Book Search

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Book Search helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at `http://books.google.com/`

399.00.570

HARVARD COLLEGE
LIBRARY

THE ESSEX INSTITUTE
TEXT-BOOK COLLECTION

GIFT OF
GEORGE ARTHUR PLIMPTON
OF NEW YORK

JANUARY 25, 1924

3 2044 097 031 884

Horace Fletcher
with best wishes

Feb. 1902 M. Foster

# A TEXT BOOK
OF
# PHYSIOLOGY

# A TEXT BOOK

OF

# PHYSIOLOGY

BY

M. FOSTER, M.A., M.D., D.C.L., F.R.S.,

PROFESSOR OF PHYSIOLOGY IN THE UNIVERSITY OF CAMBRIDGE,
AND FELLOW OF TRINITY COLLEGE, CAMBRIDGE.

ASSISTED BY

W. H. R. RIVERS, M.A., M.D.,

UNIVERSITY LECTURER IN PHYSIOLOGICAL AND EXPERIMENTAL PSYCHOLOGY
IN THE UNIVERSITY OF CAMBRIDGE.

SIXTH EDITION, REVISED.

## PART IV.

*The Senses.*

London:
MACMILLAN AND CO., LIMITED.
NEW YORK: THE MACMILLAN COMPANY.
1900

[*The Right of Translation is reserved.*]

Educ T 399.00.370

HARVARD COLLEGE LIBRARY
GIFT OF
GEORGE ARTHUR PLIMPTON
JANUARY 25, 1924

*First Edition* 1876. *Second Edition* 1877.
*Third Edition* 1879. *Fourth Edition* 1883.
*Reprinted* 1884, 1886. *Fifth Edition* 1891.
*Sixth Edition* 1900.

CAMBRIDGE: PRINTED BY J. AND C. F. CLAY,
AT THE UNIVERSITY PRESS.

# PREFACE.

THE changes in this edition are on the whole not very great, and are distributed over the greater part of the work. In making these changes I have been so largely assisted by my friend Dr Rivers, that his name fitly appears together with mine on the title-page.

We have to thank Dr Anderson for the great trouble which he has taken in reading over all the sheets.

M. FOSTER.

*November*, 1899.

# CONTENTS OF PART IV.

## BOOK III. (*continued*).

## CHAPTER III.

### SIGHT.

### SECTION I.

### ON THE GENERAL STRUCTURE OF THE EYE, AND ON THE FORMATION OF THE RETINAL IMAGE.

PAGE

§ 702. Dioptric Mechanisms and Visual Impulses . . . . . . 1253

§ 703. The General Structure of the Eye. The Formation of the Retinal Image . . . . . . . . . . . . . 1254

§ 704. A simple optic system ; its cardinal points. The refractive surfaces and media of the eye . . . . . . . . . . . 1258

§ 705. The optic constants of the Eye. The Diagrammatic Eye . . 1261

§ 706. The paths of the rays of light through the eye . . . . 1262

§ 707. The retinal image in relation to the sensations excited by it . 1264

### SECTION II.

### THE FACTS OF ACCOMMODATION.

§ 708. The eye can accommodate for far and near objects; far and near limits of accommodation . . . . . . . . . . 1265

§ 709. Scheiner's experiment . . . . . . . . . . . 1266

§ 710. Emmetropic, myopic, hypermetropic and presbyopic eyes . . 1268

§ 711. The changes observed in the eye during accommodation . . 1269

## SECTION III.

### ON THE STRUCTURE OF THE INVESTMENTS OF THE RETINA.

PAGE
§ 712. The Sclerotic Coat . . . . . . . . . . . . 1273
§ 713. The Choroid Coat . . . . . . . . . . . . 1273
§ 714. The Ciliary processes . . . . . . . . . . . 1275
§ 715. The Iris . . . . . . . . . . . . . . 1276
§ 716. The Cornea . . . . . . . . . . . . . 1277
§ 717. The Ciliary Zone . . . . . . . . . . . . 1278
§ 718. The Ciliary Muscle . . . . . . . . . . . . 1280
§ 719. The Lens . . . . . . . . . . . . . 1280
§ 720. The Vitreous Humour and the Suspensory Ligament . . . . 1281

## SECTION IV.

### THE MECHANISM OF ACCOMMODATION AND THE MOVEMENTS OF THE PUPIL.

§ 721. The mechanism for changing the anterior curvature of the lens 1283
§ 722. The evidence that such a mechanism does effect the result . 1284

### *The Movements of the Pupil.*

§ 723. Circumstances leading to constriction and to dilation of the pupil . 1287
§ 724. How constriction and dilation are brought about . . . 1287
§ 725. The nerves supplying the pupil . . . . . . . . 1288
§ 726. Constriction a reflex act by means of the optic and oculo-motor nerves . . . . . . . . . . . . . . 1290
§ 727. Changes in the pupil through the action of the cervical sympathetic nerve . . . . . . . . . . . . . . 1292
§ 728. The nature of the dilating mechanism . . . . . . . 1293
§ 729. Direct action of drugs and other agencies on the pupil . . 1295
§ 730. The nervous mechanism of accommodation . . . . . 1295
§ 731. The association of the movements of accommodation and the movements of the pupil . . . . . . . . . 1296

## SECTION V.

### IMPERFECTIONS IN THE DIOPTRIC APPARATUS.

§ 732. Imperfections of accommodation . . . . . . . . 1298
§ 733. Spherical aberration . . . . . . . . . . 1299
§ 734. Astigmatism . . . . . . . . . . . . . 1299
§ 735. Chromatic aberration . . . . . . . . . . 1301
§ 736. Entoptic phenomena . . . . . . . . . . 1302

## SECTION VI.

### THE STRUCTURE OF THE RETINA.

PAGE
§ 737. The optic nerve . . . . . . . . . . . . . 1306
§ 738. The Layers of the Retina . . . . . . . . . . 1307
§ 739. The Neuroglial Elements . . . . . . . . . . 1308
§ 740. The Nervous Elements. The rods and cones with the rod fibres and cone fibres . . . . . . . . . . . . 1310
§ 741. The inner nuclear layer . . . . . . . . . . 1313
§ 742. The layer of ganglionic cells and layer of optic fibres . . . 1315
§ 743. The probable connection of the several elements . . . . 1316
§ 744. The Macula Lutea and Fovea Centralis . . . . . . 1317
§ 745. The blood vessels of the retina . . . . . . . . 1318
§ 746. The Pigment Epithelium . . . . . . . . . . 1319

## SECTION VII.

### ON SOME GENERAL FEATURES OF VISUAL SENSATIONS.

§ 747. The relation of the sensation to the intensity of the stimulus; adaptation; Weber's law . . . . . . . . . 1322
§ 748. The relation of the sensation to the duration of the stimulus . 1325
§ 749. Flickering and continuous sensations . . . . . . . 1326
§ 750. Sensations produced by various changes in the retina referred to some external source of light . . . . . . . . 1327
§ 751. Localisation of visual sensations . . . . . . . . 1329
§ 752. The conditions of discrete visual sensations . . . . . 1330
§ 753. The region of distinct vision. The limits of distinct vision . 1331
§ 754. Nature of the discreteness of visual sensations; retinal visual units 1333

## SECTION VIII.

### ON COLOUR SENSATIONS.

§ 755. The existence of many kinds of Colour Sensations . . . 1336
§ 756. The mixing of Colour Sensations . . . . . . . . 1337
§ 757. The several usual Colour Sensations result from the mixture of simpler, primary sensations . . . . . . . . 1338
§ 758. The conditions which determine the characters of Colour Sensations 1340
§ 759. Complementary Colours . . . . . . . . . . 1341
§ 760. Any Colour Sensation produced by the suitable mixture of three Colour Sensations . . . . . . . . . . 1342
§ 761. The Young-Helmholtz theory of Colour Sensations . . . 1343
§ 762. Hering's theory of Colour Sensations. A comparison of the two theories . . . . . . . . . . . . . 1345

PAGE
§ 763. Colour Blindness in the periphery of the retina . . . . . 1351
§ 764. The influence of the yellow spot . . . . . . . . . 1352
§ 765. Variations in Colour Vision. Colour Blindness. The different kinds of Red-green Blindness . . . . . . . . . . 1352
§ 766. The explanations of Colour Blindness . . . . . . . . 1354
§ 767. The probable subjective condition of the Colour Blind . . 1356
§ 768. Yellow-blue blindness; total Colour Blindness . . . . . 1357
§ 769. Colour Sensations in relation to the intensity of the stimulus . 1358

## SECTION IX.

### On the Development of Visual Impulses.

§ 770. The Blind spot . . . . . . . . . . . . 1362
§ 771. Purkinjé's figures; their import . . . . . . . . 1363
§ 772. Possible theories as to the mode of origin of visual sensations . 1366
§ 773. Photochemistry of the retina; visual purple; its function . . 1367
§ 774. Hypothetical visual substances; insufficiency of our present knowledge . . . . . . . . . . . . . . . 1371
§ 775. The functions of the layer of rods and cones. The ophthalmoscope 1372
§ 776. Possible differences of function of rods and cones . . . 1374
§ 777. Electric currents in the retina . . . . . . . . . 1375

## SECTION X.

### On some Features of Visual Sensations, especially in relation to Visual Perceptions.

§ 778. Simultaneous visual sensations; the visual field . . . . 1376
§ 779. The psychological and physiological methods; sensations and perceptions; their want of agreement . . . . . . . 1376
§ 780. Irradiation . . . . . . . . . . . . . . 1379
§ 781. Simultaneous contrast . . . . . . . . . . . 1379
§ 782. After-images. Successive contrast. Recurrent images . . . 1380
§ 783. The phenomena of 'contrast' in their bearing on the theories of colour vision . . . . . . . . . . . . 1382
§ 784. Ocular phantoms or hallucinations . . . . . . . 1386

## SECTION XI.

### Binocular Vision.

§ 785. The movements of the eyeball; their limitations. Centre of rotation, visual axis, visual plane . . . . . . . . . 1388

PAGE
§ 786. The visual field and field of sight of one eye and of both eyes . 1389
§ 787. Corresponding or Identical Points. Double vision . . . 1391
§ 788. The movements of the eyeball; the primary position and secondary positions; the kind of movements which are possible . . . 1394
§ 789. Listing's Law; the experimental proof . . . . . . . 1395
§ 790. The muscles of the eyeball . . . . . . . . . . 1398
§ 791. The action of the ocular muscles . . . . . . . . . 1399
§ 792. The nervous mechanism of the movements of the eyeballs; the coordination of the movements . . . . . . . . . 1402
§ 793. The nervous centres for the movements of the eyeballs . . 1405
§ 794. The Horopter . . . . . . . . . . . . . 1407

## SECTION XII.

### On some Features of Visual Perceptions and on Visual Judgments.

§ 795. On the differences between the objective field of sight and the subjective field of vision . . . . . . . . . . 1409
§ 796. The psychical processes belonging to visual perceptions; illusions and visual judgments . . . . . . . . . . . 1411
§ 797. Appreciation of apparent size . . . . . . . . . 1412
§ 798. Perception of distance and of actual size . . . . . . 1413
§ 799. The perception of solidity . . . . . . . . . . 1416
§ 800. The struggle of the two fields of vision . . . . . . 1418

## SECTION XIII.

### The Nutrition of the Eye.

§ 801. The arrangement of the blood vessels . . . . . . . 1419
§ 802. The vaso-motor changes in the eye . . . . . . . . 1420

*The Lymphatics of the Eye.*

§ 803. The lymphatic vessels and lymph spaces of the eye . . . 1420
§ 804. The aqueous humour; the changes taking place in it; how effected 1422
§ 805. The vitreous humour; the changes taking place in it . . 1424

## SECTION XIV.

### The Protective Mechanisms of the Eye.

§ 806. The eyelids and their muscles . . . . . . . . . 1426
§ 807. The conjunctiva and its glands. Tears. The secretion of tears 1427

## CHAPTER IV.

### HEARING.

### SECTION I.

### ON THE GENERAL STRUCTURE OF THE EAR AND ON THE STRUCTURE AND FUNCTIONS OF THE SUBSIDIARY AUDITORY APPARATUS.

PAGE
§ 808. The embryonic history of the Ear. The otic vesicle . . . 1430
§ 809. The general relations of the parts of the Ear; vestibule and cochlea, membranous and bony labyrinth, tympanum, auditory ossicles, membrana tympani and external meatus . . . . . . 1431
§ 810. The general use of the several parts . . . . . . . 1434

*The Conducting Apparatus of the Tympanum.*

§ 811. The auditory ossicles . . . . . . . . . . . 1435
§ 812. The tympanum; its structure and relations . . . . . 1436
§ 813. The membrana tympani . . . . . . . . . 1439
§ 814. The joints, ligaments, and positions of the auditory ossicles . 1441
§ 815. The chain of ossicles as a lever . . . . . . . . 1443

*The Conduction of Sound through the Tympanum.*

§ 816. Longitudinal and transversal sonorous vibrations. The vibrations of the tympanic membrane . . . . . . . . . 1444
§ 817. The conduction of vibrations through the chain of ossicles . 1446
§ 818. The conduction of vibrations through the bones of the skull . 1447
§ 819. The action of the tensor tympani and stapedius muscles . . 1448
§ 820. The Eustachian tube . . . . . . . . . . . 1450

### SECTION II.

### THE STRUCTURE OF THE LABYRINTH.

§ 821. The parts of the vestibule; utricle, saccule and semicircular canals 1452
§ 822. The perilymph cavity of the vestibule . . . . . . . 1454
§ 823. The auditory nerve; the maculæ and cristæ acusticæ . . . 1455
§ 824. The general structure of the Cochlea . . . . . . . 1456

*The Vestibular Labyrinth.*

§ 825. The minute structure of the parts free from nerve endings . 1460
§ 826. The structure of the cristæ acusticæ . . . . . . . 1460

PAGE
§ 827. The constituent cells; cylinder or hair cells, rod or spindle cells 1462
§ 828. The structure of the maculæ acusticæ . . . . . . . 1463
§ 829. The otoconia and otoliths . . . . . . . . . . 1464

*The Cochlea.*

§ 830. The Canalis Cochlearis, its several parts . . . . . . 1464
§ 831. The basilar membrane . . . . . . . . . . . 1466
§ 832. The organ of Corti . . . . . . . . . . . 1467
§ 833. The rods of Corti . . . . . . . . . . . . 1469
§ 834. The inner hair cells . . . . . . . . . . . 1471
§ 835. The outer hair cells . . . . . . . . . . . 1472
§ 836. The endings of the cochlear nerve . . . . . . . 1473
§ 837. The tectorial membrane . . . . . . . . . . 1475
§ 838. The differences of the organ of Corti in different parts of the spiral 1475
§ 839. Measurements of some parts of the cochlea . . . . . 1476

## SECTION III.

### On Auditory Sensations.

§ 840. Noises and Musical Sounds . . . . . . . . . . 1477
§ 841. The characters of musical sounds; loudness, pitch and quality; fundamental and partial tones . . . . . . . . 1477
§ 842. The limits of auditory sensations . . . . . . . . 1479
§ 843. Appreciation of differences of pitch . . . . . . . 1480
§ 844. The number of vibrations needed to excite a sensation . . 1480
§ 845. The characters of noises . . . . . . . . . . 1481
§ 846. The effects of exhaustion . . . . . . . . . . 1482
§ 847. The fusion of auditory sensations . . . . . . . . 1483
§ 848. The interference of vibrations. Beats . . . . . . . 1483

## SECTION IV.

### On the Development of Auditory Impulses.

§ 849. The transmission of impulses through the labyrinth; the functions of the hairs and otoliths . . . . . . . . . 1487
§ 850. The analysis of complex waves of sound; theories as to the mode of action of the organ of Corti . . . . . . . . . 1489
§ 851. The appreciation of the nature of sounds ultimately a psychical process . . . . . . . . . . . . . . 1493
§ 852. Probable functions of the vestibular labyrinth . . . . 1494

## SECTION V.

### ON AUDITORY PERCEPTIONS AND JUDGMENTS.

PAGE
§ 853. Auditory phantoms . . . . . . . . . . . . 1496
§ 854. The appreciation of outwardness in sounds is connected with the tympanum . . . . . . . . . . . . . . 1497
§ 855. Hearing binaural. The judgment of the direction of sounds . 1498
§ 856. Judgment of the distance of sounds . . . . . . . 1499

## CHAPTER V.

### TASTE AND SMELL.

## SECTION I.

### THE STRUCTURE OF THE OLFACTORY MUCOUS MEMBRANE.

§ 857. The structure of olfactory mucous membrane, cylinder cells and rod cells . . . . . . . . . . . . . 1501
§ 858. The termination of the olfactory fibres . . . . . . 1503

## SECTION II.

### OLFACTORY SENSATIONS.

§ 859. The sensation due to contact of particles with the membrane . 1504
§ 860. The chief characters of olfactory sensations . . . . 1505
§ 861. Olfactory judgments. The olfactory nerve the nerve of smell . 1507

## SECTION III.

### THE STRUCTURE OF THE ORGANS OF TASTE.

§ 862. The structure of the lining membrane of the mouth . . . 1508
§ 863. Papillæ foliatæ; taste buds, rod cells, and subsidiary cells. The distribution of taste buds . . . . . . . . . . 1509

## SECTION IV.

### GUSTATORY SENSATIONS.

§ 864. Sensations of taste usually or frequently accompanied by other sensations. Chemical constitution of sapid substances . . 1513
§ 865. The different kinds of taste. Sensations of taste provoked by mechanical and electrical stimulation . . . . . . . 1513
§ 866. The conditions under which taste sensations are excited . . 1515
§ 867. The distribution of the several kinds of tastes. Theories as to the mode of origin of taste sensations . . . . . . 1516
§ 868. The nerves of taste; the chorda tympani . . . . . . 1520

## CHAPTER VI.

### ON CUTANEOUS AND SOME OTHER SENSATIONS.

### SECTION I.

### THE NERVE ENDINGS OF THE SKIN.

PAGE
§ 869. General and special nerve endings. End-bulbs . . . . . 1522
§ 870. Pacinian corpuscles . . . . . . . . . . . . 1523
§ 871. Grandry's corpuscles . . . . . . . . . . . . 1525
§ 872. Touch corpuscles . . . . . . . . . . . . . 1525
§ 873. Nerve endings in the cornea . . . . . . . . . . 1527
§ 874. Nerve endings in the epidermis . . . . . . . . . 1527
§ 875. 'Touch cells' in the epidermis and elsewhere . . . . . 1528

### SECTION II.

### THE GENERAL FEATURES OF CUTANEOUS SENSATIONS.

§ 876. Three kinds of cutaneous sensations, of pressure, of heat and cold, and of pain . . . . . . . . . . . . . . 1529

*Tactile Sensations or Sensations of Pressure.*

§ 877. The general characters of tactile sensations. Touch points. . 1529
§ 878. The localisation of tactile sensations . . . . . . . 1531

*Sensations of Heat and Cold.*

§ 879. Sensations of heat and cold due to sudden changes in the temperature of the skin . . . . . . . . . . 1533
§ 880. The general characters of temperature sensations. Heat and cold points . . . . . . . . . . . . . . 1534
§ 881. Tactile and temperature sensations in parts other than the external skin . . . . . . . . . . . . . . . 1536

### SECTION III.

### ON PAINFUL AND SOME OTHER KINDS OF SENSATION.

§ 882. Sensations of pain distinct from other sensations . . . 1537
§ 883. Sensations of pain are extreme degrees of common sensibility . 1537
§ 884. Special nerve endings not necessary for sensations of pain . . 1540
§ 885. Hunger and thirst . . . . . . . . . . . . 1541

## SECTION IV.

### On the mode of Development of Cutaneous Sensations.

PAGE
§ 886. The specific energy of nerves. Special terminal organs necessary for the sensations of touch and temperature as distinguished from sensations of pain . . . . . . . . . . 1544
§ 887. The terminal organs for sensations of pressure different from those for sensations of temperature . . . . . . . . 1547
§ 888. The terminal organs for sensations of heat different from those for sensations of cold . . . . . . . . . . . 1548
§ 889. The importance of contrast in cutaneous sensations . . . 1549
§ 890. The nature of the terminal organs . . . . . . . 1550

## SECTION V.

### The Muscular Sense.

§ 891. We possess a sense of 'movement,' of 'position,' and of 'effort' 1552
§ 892. The muscular sense distinguished from the sense of effort . . 1553
§ 893. The afferent impulses forming the basis of the muscular sense are distinct from cutaneous impulses . . . . . . 1554
§ 894. They are derived from the joints, muscles, ligaments, and tendons 1556

## SECTION VI.

### On Tactile Perceptions and Judgments.

§ 895. The ties between touch and the muscular sense . . . . 1559
§ 896. The ties between touch and sight . . . . . . . 1560
§ 897. Cutaneous sensations may arise otherwise than from cutaneous events . . . . . . . . . . . . . . 1561
§ 898. Tactile Illusions . . . . . . . . . . . . 1562

Index . . . . . . . . . . . . . . . 1563

# LIST OF FIGURES IN PART IV.

FIG. PAGE

143. Diagrammatic outline of a horizontal section of the eye to illustrate the relations of the various parts . . . . . . . . 1255

144. Diagram of simple optical system . . . . . . . . 1259

145. Diagram of the schematic or diagrammatic eye . . . . 1262

146. Diagram of the formation of a retinal image . . . . 1263

147. Diagram of Scheiner's experiment . . . . . . . . 1267

148. Diagram of images reflected from the eye . . . . . . 1271

149. Diagram of the ciliary muscle as seen in a vertical radial section of the ciliary region . . . . . . . . . . 1279

150. Diagram to illustrate accommodation . . . . . . . 1284

151. Diagrammatic representation of the nerves governing the pupil . 1289

152. Diagram illustrating chromatic aberration . . . . . . 1302

153. Diagram to illustrate entoptical images . . . . . . . 1304

154. Diagram to illustrate the structure of the retina . . . . 1311

155. Diagram of three primary colour sensations . . . . . 1344

156. Diagram to illustrate Hering's theory of colour vision . . . 1347

157. Diagram illustrating the formation of Purkinjé's figures when the illumination is directed through the sclerotic . . . . 1364

158. Diagram illustrating the formation of Purkinjé's figures when the illumination is directed through the cornea . . . . 1365

159. Diagram to illustrate the principles of a simple form of ophthalmoscope . . . . . . . . . . . . . 1374

160. Figure to illustrate irradiation . . . . . . . . 1279

161. Figure to illustrate influence of contrast on flicker . . . 1384

162. The visual field of the right eye . . . . . . . . 1389

163. The visual fields (fields of sight) of the two eyes when the eyes converge to the same fixed point . . . . . . 1390

164. Diagram illustrating corresponding points . . . . . . 1392

165. Figure to illustrate the insertions of the ocular muscles . . 1398

166. Diagram to illustrate the actions of the ocular muscles . . 1400

167. Diagram illustrating a simple horopter . . . . . . . 1407

FIG. PAGE
168. Figure to illustrate the appreciation of apparent size . . . 1412
169. The same . . . . . . . . . . . . . . . 1412
170. Figure to illustrate an optical effect produced by parallel slanting lines . . . . . . . . . . . . . . . 1413
171. Figure to illustrate binocular vision . . . . . . . 1417
172. Diagram to illustrate the general structure of the ear . . . 1432
173. The bony labyrinth . . . . . . . . . . . . 1433
174. The auditory ossicles . . . . . . . . . . . 1436
175. Diagram to illustrate the relations of auditory passage, tympanum and Eustachian tube . . . . . . . . . . 1437
176. Diagram of the median wall of the tympanum . . . . 1437
177. Diagram of the outer wall of the tympanum as seen from the mesial side . . . . . . . . . . . . . . . 1438
178. Frontal section through the tympanum . . . . . . 1439
179. The membrana tympani . . . . . . . . . . . 1440
180. The ossicles in position . . . . . . . . . . 1441
181. The ligaments of the ossicles . . . . . . . . . 1442
182. The stapes in position . . . . . . . . . . . 1443
183. The malleus and incus in position . . . . . . . . 1444
184. Diagram of the outer wall of the tympanum as seen from the mesial side . . . . . . . . . . . . . . . 1449
185. The membranous labyrinth as seen from above . . . . 1452
186. The membranous labyrinth and the endings of the auditory nerve . 1453
187. Diagram of a transverse section of a whorl of the cochlea . . 1457
188. Diagram to illustrate the structure of a crista or a macula . 1461
189. Diagram of the organ of Corti . . . . . . . . 1467
190. Diagram of the constituents of the organ of Corti . . . 1469

# CHAPTER III.

## SIGHT.

### SEC. 1. ON THE GENERAL STRUCTURE OF THE EYE, AND ON THE FORMATION OF THE RETINAL IMAGE.

§ **702.** IN dealing with the brain we have been incidentally obliged to deal with some of the facts connected with the senses; but we must now study the details of the subject. And, for the very reason that it is the most highly developed and differentiated sense, it will be convenient to begin with the sense of sight; we shall find that the study of it throws more light on the simpler and more obscure senses than the study of them throws on it.

A ray of light entering the eye and falling on the retina gives rise to what we call a sensation of light; but in order that distinct vision of any object emitting or reflecting rays of light may be gained, an image of the object must be formed on the retina, and the better defined the image the more distinct will be the vision. Hence in studying the physiology of vision, our first duty is to examine into the arrangements by which the formation of a satisfactory image on the retina is effected; these we may call briefly the dioptric mechanisms. We shall then have to inquire into the laws according to which rays of light impinging on the retina give rise to nervous impulses, and into the laws according to which the sensory impulses thus generated, which we will call visual impulses, give rise in turn to visual sensations. Here we shall come upon the difficulty of distinguishing between the events which are of physical origin, due to changes in the retina and optic fibres, and those which are of psychical origin, due to features of our own consciousness; for many of our conclusions are based on an appeal to consciousness. Moreover, in appealing to our own consciousness we meet with the further difficulty that, at least in

'7x

most cases, what we may speak of as the primary and simple affections of consciousness directly and immediately resulting from the stimulation of the retina are more or less modified by secondary affections of consciousness, to which the former through the intricate workings of the central nervous system give rise, or by concomitant affections or conditions of consciousness. We may speak of the simpler affections as visual sensations; the more complex affections receive various names, such as visual perceptions, visual judgments. When in familiar language we say that we 'see' this or that, we are for the most part really referring not to simple sensations but to more complex affections of consciousness.

§ **703**. In the structure of the eye we may distinguish two parts: the one is the retina, in which visual impulses are generated; the other comprises all the rest of the eyeball, for all the other structures serve either as a dioptric mechanism or as a means of nourishing the retina. This distinction is readily seen when we trace out the early history of the eye.

The first of the three primary cerebral vesicles (§ 600), that which is the forerunner of the third ventricle, buds out on each side the stalked and hollow optic vesicle. The wall of this optic vesicle, like that of the rest of the medullary tube, consists of epithelium, and the cavity of the vesicle is at first continuous, through the canal of the hollow stalk, with that of the medullary tube. The whole is covered over by the layer of epiblast which, with scanty underlying mesoblast, is the rudiment of the future skin.

Very soon the vesicle is doubled back upon or folded in upon itself so that the originally more or less spherical hollow single-walled vesicle is converted into a more or less hemispherical cup with a double wall, one the hind or outer wall corresponding to the hind half, and the other the front or inner wall to the front half of the vesicle, the two walls of the cup coming eventually into contact so that the cavity of the vesicle is obliterated. The folding is somewhat peculiar, inasmuch as it takes place not only at the front but also and indeed chiefly at the side, forming at the side a cleft, the choroidal fissure, the edges of which ultimately unite. We cannot enter into the details of the matter here, and indeed only refer to the character of the folding in order to point out that it involves the stalk as well as the cup. The stalk is first flattened and then doubled up lengthwise, a quantity of mesoblastic tissue being thrust into the hollow of the fold; and eventually the originally hollow stalk becomes a solid stalk having within it a core of mesoblastic tissue, carrying blood vessels. This core of vascular mesoblast, the origin of the future central artery of the retina, is continuous with a quantity of mesoblast which enters into the hollow of the cup at the time of folding, and, as we shall see, the central artery of the stalk is up to a certain stage of development carried forward through the centre of the cup. The cup becomes what we may speak of broadly as the retina, and we may call it the *optic* or *retinal* cup; the solid stalk becomes the optic nerve; and the other parts of the eyeball are formed round this retinal cup, which remains as the essential part of the eye.

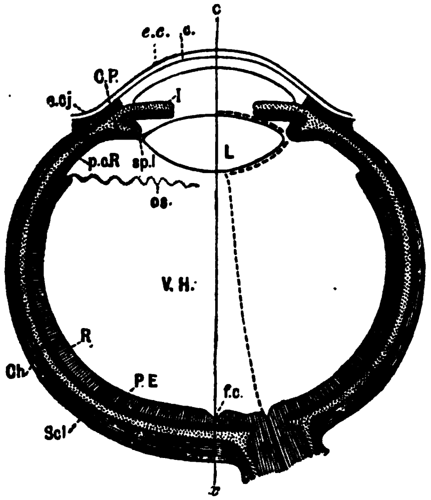

FIG. 143. DIAGRAMMATIC OUTLINE OF A HORIZONTAL SECTION OF THE EYE, TO ILLUSTRATE THE RELATIONS OF THE VARIOUS PARTS.

The figure is to be regarded as very diagrammatic, more or less distortion of the relative sizes of the various parts and of the relative thickness of the coats being unavoidable in the effort to secure simplicity.

*Scl.* the sclerotic coat, shaded longitudinally, continuous with the (unshaded) body of the cornea. *e.c.* the epithelium of the cornea continuous with *e.cj.* the epithelium of the conjunctiva.

*Ch.* the choroid coat, with *C.P.* the ciliary process and *I.* the body of the iris, all stippled to indicate that they are all parts of the same vascular investment.

*R.* the retina or inner wall, and *P.E.* the pigment epithelium or outer wall of the retinal cup. In front of the wavy line *OS.*, marking the position of the ora serrata, the retina proper changes into the pars ciliaris retinæ, *p.c.R.* Both the pigment epithelium and the pars ciliaris retinæ are represented as continued over the back of the iris as well as over the ciliary process.

*L.* the lens. *sp.l.* the suspensory ligament. The broken line round the lens, shewn on one side only, represents the membrana capsulo-pupillaris; and the straight continuation of it through *V.H.* the vitreous humour to *O.N.* the optic nerve indicates the embryonic continuation of the central artery of the retina.

*o.x.* the optic axis, in this case made to pass through the fovea centralis *fc.*

The front or inner wall of the retinal cup is from the first distinctly thicker than the hind or outer wall (Fig. 143); it soon consists of more than one layer of epithelium, and it alone, or, more strictly speaking, part of it alone, becomes the retina proper.

The hind or outer wall remains thin, and continues to consist of a single layer of epithelium, the cells of which are never developed into nervous elements but soon become loaded with pigment, and the greater part of it is known in the adult eye as the pigment epithelium of the retina, which, as we shall see, is in close functional connection with the nervous elements of the retina proper. At the time when the epithelial cells of the stalk of the retinal cup are developed into the fibres of the optic nerve, these become connected with the elements of the inner or retinal wall only of the cup; they pierce the outer wall of pigment epithelium, making no connections with the cells of that outer wall.

The retina then, in which by the action of light visual impulses are generated, is in reality a part of the brain, removed to some distance from the rest of the brain but remaining connected with it by means of the tract of white matter which we call the optic nerve; and, as we shall see, the retina is in structure similar to parts of the grey matter of the brain. The optic nerve is not like other nerves an outgrowth from the central nervous system, but like the olfactory tract (§ 674) a commissure of white matter between two parts of the brain, namely, between the outlying retina and the internally placed corpus geniculatum, pulvinar, and corpus quadrigeminum. We shall find accordingly that in structure it differs from ordinary cranial or spinal nerves.

Into the mouth of the retinal cup there is thrust a rounded mass of epithelium, an involution from the superficial epiblast; this becomes the lens. The hollow of the retinal cup is occupied, as we have said, by mesoblast; this ultimately becomes modified into the vitreous humour. The mesoblastic tissue surrounding the cup is developed into an investment of two coats; an inner, somewhat loose and tender, vascular and in part muscular coat, which on the one hand serves to nourish the retina, and on the other hand carries out certain movements of the dioptric apparatus, and an outer, firmer and denser coat, which affords protection to the whole of the structures within. The inner vascular coat, which may be compared to the pia mater, is called the *choroid* (Fig. 143 *Ch.*), and in the front part of the eye, at about the level of the lens, is thrown into a number of radiating folds or plaits, the ciliary processes *C.P.* The outer coat, which may be compared to the dura mater, is called the *sclerotic* (Fig. 143 *Scl.*). Over the greater part of the eyeball the two coats are in apposition, or separated only by narrow lymphatic spaces, which may be compared with the subarachnoid spaces, but towards the front they diverge; the choroid is bent inwards towards the central axis of the eye to form the diaphragm called the *iris* (Fig. 143 *I.*), while the sclerotic is continued forwards to form, beneath the epidermis into which the superficial epiblast is developed, the basis of the *cornea* (Fig. 143 *C.*). At the angle of divergence of the two coats is developed a small mass of muscular fibres, the ciliary muscle, of which we shall speak in detail presently.

The inner or front wall of the retinal cup becomes, as we have said, thick, and is developed into the retina; but this takes place only over about the hind three-fourths of the cup. Along a meridian round the eye, at a wavy boundary line called the *ora serrata* (Fig. 143 *O.S.*), the retina proper ceases and the inner wall of the retinal cup in front of the ora serrata is continued on as a much thinner structure (Fig. 143 *p.c.R.*) consisting of a single layer only of cells; this is spoken of as the *pars ciliaris retinæ.* The outer or hind wall of the retinal cup consists throughout of a single layer of epithelium cells loaded with pigment. Behind the ora serrata, that is, in the region of the retina proper, these cells have, as we shall see, peculiar features, but in front of the ora serrata they lose these features and become ordinary cubical cells, though still loaded with pigment.

Hence the choroid may be described as having a double lining. Over the hind part of the eye, behind the ora serrata, it is lined by the single layer of pigment epithelium and the retina. In front of the ora serrata it, including the ciliary processes, is lined by the same layer of pigment epithelium representing the outer wall, and by the single layer of cells, free from pigment, representing the inner wall of the retinal cup, the latter being called, as we have said, the pars ciliaris retinæ. And as the ciliary part of the choroid passes on to form the iris, these two layers are also continued on to line the back of the iris, coming to an end at the margin of the pupil or central opening of the iris, which may accordingly be taken as marking the extreme lip of the retinal cup (Fig. 143). Here however, as we shall see, the two layers are not so easily and distinctly recognised as in the ciliary region; and the nature of the structures forming the back of the iris has been a matter of much controversy.

At an early stage the mesoblastic tissue, which fills up the hollow of the retinal cup and surrounds the lens, is continuous at the mouth of the retinal cup with the outer investment of the cup; it here forms around the lens the *membrana capsulo-pupillaris*, and at the margin of the iris the *membrana pupillaris* blocking up the future opening of the pupil. The arteria centralis retinæ, which during the folding of the cup and stalk is carried into the core of the optic nerve, does not at this early stage stop at the retina, but is continued forward through the middle of the vitreous humour to the membrana capsulo-pupillaris, and furnishes the developing lens with an abundant supply of blood. But neither layer of the retinal cup stretches over the pupillary membrane; they both stop, as we have said, at the margin of the iris. Before birth takes place, the membrana pupillaris is, in man, absorbed and the pupil is thus established; at the same time the central artery in the vitreous humour is obliterated beyond the retina, and the vascular membrana capsulo-pupillaris gives place to the non-vascular capsule of the lens and the suspensory ligament of which we shall speak hereafter.

Between the iris, which is the extreme front of the choroid investment, and the cornea, which is the extreme front of the sclerotic investment, the lymphatic spaces which over the rest of the eye are narrow and linear are developed into a large conspicuous chamber, the *anterior chamber* of the eye, which upon the establishment of the pupil by the absorption of the pupillary membrane becomes continuous with the smaller "posterior chamber" of the eye, or space between the back surface of the iris and ciliary processes on the outside and the suspensory ligament with the lens on the inside. The cavity of the conjoined anterior and posterior chambers, being a continuation and enlargement of the flatter spaces between the choroid or pia mater of the eye, and sclerotic or dura mater of the eye, may be likened to the subarachnoid space, and like that space contains a peculiar fluid; this, which is called the aqueous humour, like the cerebro-spinal fluid, differs from ordinary lymph, and is probably, to a large extent, furnished by the ciliary processes in some such way as the cerebrospinal fluid is furnished by the choroid plexuses (§ 695).

## *The Formation of the Retinal Image.*

§ **704.** The iris and choroid coat contain, as we have said, muscular elements, and by means of these muscular elements changes in the form and relations of some of the parts of the eye are brought about; hence we have to distinguish between the eye at rest, and the eye which is undergoing one or other of these changes. It will be convenient to reserve what we have further to say concerning the histological and other details of structure of these parts until we come to deal with these changes; and, simply premising that the cornea and lens are transparent bodies with surfaces of certain curvatures, we may at once pass to the consideration of the dioptrics of the eye at rest.

The eye is a camera, consisting of a series of surfaces and media arranged in a dark chamber, the iris serving as a diaphragm; and the object of the apparatus is to form on the retina a distinct image of external objects. That a distinct image is formed on the retina may be ascertained by removing the sclerotic from the back of an eye, and looking at the hinder surface of the transparent retina while rays of light proceeding from an external object are allowed to fall on the cornea. To understand how such an image is formed, we must call to mind a few optical principles.

A dioptric apparatus in its simplest form consists of two media of different refractive power separated by a (spherical) surface; and the optical properties of such an apparatus depend upon

(1) the curvature of the surface, (2) the relative refractive powers of the media.

Such a simple optical system is represented in Fig. 144, where *apb* represents, in section, a curved (spherical) surface separating a less refractive medium on the left hand towards *O*, from a more refractive medium on the right hand towards *A*. The surface in question is symmetrically placed as regards the line *OA*, which falling normal (perpendicular) to the surface at *p* passes through the centre *n* of the sphere with whose surface we are dealing. This line is called the *optic axis*.

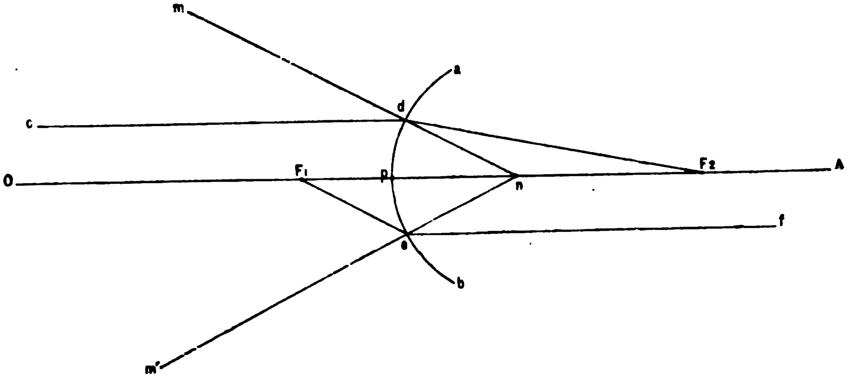

FIG. 144. DIAGRAM OF SIMPLE OPTICAL SYSTEM.

All rays of light which, in passing from the first less refractive to the second more refractive medium, cut the surface normally, such as the one, *Op*, in the line of the optic axis, and others, such as *md, m'e,* undergo no refraction; all such rays are continued on as straight lines, and all pass through *n*, the centre of the sphere or *nodal point.* All other rays passing from the first to the second medium are refracted. Of these all those which lie in the first medium parallel to the optic axis, such as *cd,* are so refracted as to meet in the second medium at a point, $F_2$, on the optic axis; this is called the *principal posterior* (or second) *focus.* On the optic axis in the first medium there is another important point, $F_1$, the rays of light passing from which, such as $F_1e$, are so refracted in passing into the second medium as to become parallel, *ef*, to the optic axis; this point is called the *principal anterior* (or first) *focus.* The point at which the optic axis cuts the surface is, for reasons which we shall see presently, called the *principal point.* The above points, viz. the posterior and the anterior principal foci, the nodal point, and the principal point are the *cardinal points* of such an optical system.

Such a simple system, however, does not represent the optical conditions of the eye, for this consists of several media bounded by several surfaces, the latter differing from each other in curvature, though being approximately spherical. Rays of light in passing from an external object to the retina traverse in succession the following surfaces and media:—the anterior surface of the cornea, the substance of the cornea, the posterior surface of the cornea, the aqueous humour, the anterior surface of the lens, the substance of the lens, the posterior surface of the lens, and the vitreous humour; so that we have to deal with four surfaces, and, including the external air, four media. Indeed the matter is in reality still more complicated, for the structure of the lens, as we shall see, is such that the substance of the lens differs somewhat in refractive power in different parts, the central parts being more refractive than the peripheral parts; moreover, the lens is covered in front by a capsule different in structure from the lens itself. We may, however, neglect, without fear of serious error, these smaller differences, and consider the lens as one medium of uniform refractive power bounded by an anterior and a posterior surface. The cornea again, as we shall see, is not absolutely uniform in structure, but this we may also neglect and consider the cornea as a medium, also of uniform refractive power, bounded by an anterior and a posterior surface. Moreover, the posterior surface of the cornea is parallel to (concentric with) the anterior surface or nearly so. Now when the two surfaces which bound a medium are parallel to each other we may, in dealing with refraction, neglect the thickness of the medium entirely, we may suppose it to be absent and treat the two surfaces as if they were one. We may therefore, without serious error, neglect the substance of the cornea, and consider the cornea as affording one surface, its anterior surface, bounding the air in front from the aqueeus humour behind. Lastly, the aqueous humour differs in refractive power so little from the vitreous humour that we may consider the two as forming one medium.

We have therefore to deal with three surfaces separating three media, viz.:—first, the anterior surface of the cornea, at which considerable refraction takes place as the rays of light pass from the less refractive air into the more refractive aqueous humour; secondly, the anterior surface of the lens, at which again considerable refraction takes place as the rays pass from the less refractive aqueous humour into the more refractive substance of the lens; and lastly, the posterior surface of the lens, at which refraction takes place as the rays pass from the more refractive substance of the lens into the less refractive vitreous humour. The three surfaces, differing in curvature, are all approximately centred, symmetrically disposed around, the optic axis of the system. This optic axis, in the majority of eyes, meets the retina, not quite at that part of it which, under the name of *fovea centralis*, we shall hereafter speak of as the centre of the retina, but a little above and to the nasal side of that part.

§ **705**. The eye, therefore, even with the simplifications which we have introduced, presents a much more complex optical system than the one described above. It has, however, been shewn mathematically that a complex optical system consisting of several surfaces and media centred on one optical axis may be treated as if it were a more simple system consisting of two surfaces only. In such a simplified system the two (ideal) surfaces have an anterior and a posterior principal focus, and each surface has its own nodal point; moreover, the two points where the two surfaces cut the optic axis are called *principal points* (and vertical planes drawn through those points *principal planes*), first or anterior, and second or posterior. Hence the cardinal points of such a simplified complex system are six in number, namely, the anterior and posterior principal foci, the anterior and posterior principal points, and the anterior and posterior nodal points. (When such a system is, by removal of surfaces and media, converted into the still more simple system of one surface separating two media, the two nodal points become coincident in one point, namely, the centre of the sphere, and the two principal points become coincident in one point, namely, the point at which the optic axis cuts the surface.)

In order to effect such a simplification of a complex optical system, it is requisite to know:—(1) The refractive index of each medium. (2) The radius of curvature of each surface. (3) The distance along the optic axis between the first surface on which the rays fall and the succeeding surfaces. These can be and have been determined for the human eye, and the following table gives the several values usually adopted, with some recent corrections, the latter being placed in brackets.

| | | |
|---|---|---|
| Refractive index of aqueous or vitreous humour... | 1·3376 (1·3365) | |
| Mean refractive index of lens ........................ | 1·4545 (1·4371) | |
| Radius of curvature of cornea ........................ | 8 (7·829) | mm. |
| „ „ of anterior surface of lens ... | 10 | „ |
| „ „ of posterior „ „ .... | 6 | „ |
| Distance from anterior surface of cornea to anterior surface of lens .................................. | 4 (3·6) | „ |
| Thickness of lens .......................................... | 4 (3·6) | „ |

By means of these measurements the optical system of the eye may be simplified into an optical system of two surfaces. In this 'schematic, or diagrammatic, eye of Listing,' as it is generally called, the two (ideal) surfaces, and the principal points where these cut the optic axis (Fig. 145, $p^1$, $p^2$, the two surfaces being indicated by dotted lines), lie close together in the front part of the aqueous humour, and the nodal points, $n^1$, $n^2$, lie, also close together, in the back part of the lens.

Further, the two principal surfaces lie so close together that, for practical purposes, no serious error is introduced, if instead of two such surfaces we assume the existence of one surface lying midway between the two. In this way we arrive at the 'reduced diagrammatic eye,' or 'the reduced eye' as it is called, in which the several surfaces and media of the actual eye are replaced by one (ideal) spherical surface (Fig. 145 *P*), having one nodal point, *N*; the two media which the surface separates are supposed to be air on the one side and water on the other.

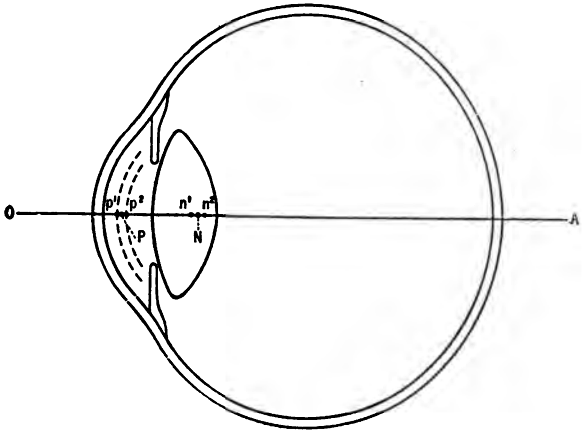

Fig. 145. Diagram of the Schematic or Diagrammatic Eye.

The several positions of the cardinal points of this 'reduced eye' are as follows:

The *principal point*, where the one surface of the system cuts the optic axis, lies in the aqueous humour, 2·3448 mm. behind the anterior surface of the cornea.

The *nodal point* lies in the back part of the lens, ·4764 mm. in front of the posterior surface of the lens.

The *posterior principal focus* lies 22·647 (22·819) mm. behind the anterior surface of the cornea, that is to say, practically lies on the retina.

The *anterior principal focus* lies 12·8326 mm. in front of the anterior surface of the cornea.

The *radius of curvature* of the (ideal) surface is 5·1248 mm.; (that of the cornea is 8 mm., and of the anterior surface of the lens 10 mm.).

§ **706.** By help of this 'reduced eye' we are enabled to trace out the paths of rays of light through the actual eye, and to study the formation of images on the retina. When an image of an external object, such as an arrow (Fig. 146), is formed in such an eye, each point of the object is considered as sending out a pencil of diverging rays, which by the system are made to converge again into the point in the image which corresponds to the point in the object. One such pencil of rays proceeds from the point at the extreme tip of the arrow, another from the extreme point at the other end, and other pencils from all the points between these two. Each such pencil has for its core a ray called the *principal ray, a, a′*, around which are arranged, with increasing divergency, the other rays of the pencil, such as *b, b′, c, c′*. When such a pencil of rays falls on the refracting surface, such as the 'principal surface' of the reduced eye, the principal ray of the pencil, *a*, being normal to that surface, is not refracted at all, but passes straight on through the nodal point *n*, while the other rays of the pencil, *b, c*, undergoing refraction according to their respective divergences, are made to converge together at some point on the path of the principal ray, and thus form at that spot the image of the point from which the pencil proceeded. The exact position on the line of the principal ray, at which convergence takes place and at which the image is formed, will depend on the refractive power of the optical system in relation to the amount of divergence of the pencil; the refractive power of the system remaining the same, it will be nearer to, or farther from, the nodal point according as the rays are less or more divergent; and the divergence of the rays remaining the same, it will be nearer to, or farther from, the nodal point according as the refractive power of the system is greater or less.

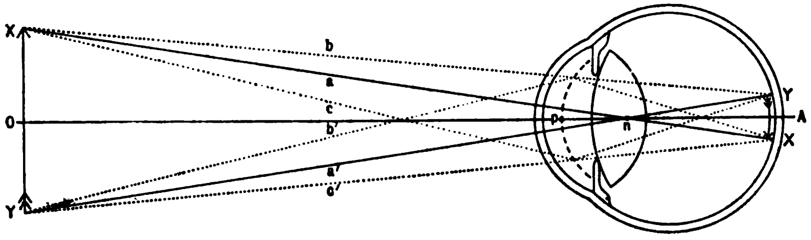

FIG. 146. DIAGRAM OF THE FORMATION OF A RETINAL IMAGE.

Hence supposing the eye to be in that condition in which a distinct image of the arrow is formed on the retina, we can find the position on the retina of the image of the extreme point of the tip of the arrow, by simply drawing a straight line from that extreme point of the arrow *X* through the nodal point *n* of the 'reduced' eye. Such a straight line represents the path of the 'principal ray' of the pencil proceeding from the extreme tip of the arrow, and when an image is formed on the retina the other diverging rays of that pencil will be so refracted as to converge at the point *x*, where that line meets the retina; all the rays will form together there the image of the extreme point of the arrow. In a similar way a straight line drawn through the nodal point from the extreme point of the other end of the arrow, and continued until it meets the retina at *y*, will give us the position of the image of the other end of the arrow; and in like manner lines drawn from other points of the arrow through the same nodal point will give us the position on the retina of the images of those other points. In this way the construction of the reduced eye enables us to ascertain the position, magnitude, and features of the retinal image of an object.

§ **707.** A ray of light, that is to say a series of waves of ether, falling upon a point of the retina stimulates certain structures in the retina and gives rise, as we have said, to visual impulses and so to a sensation of light; this we may consider as a visual sensation in its simplest form. When a number of different points of the retina are thus stimulated at the same time, as when an image of an external object falls in proper focus on the retina, the total result is a complex group of visual impulses and thus a complex sensation, by which we perceive, as we say, the object; and this complex sensation is sometimes spoken of as a visual image corresponding to the retinal image. Such a term is not a desirable one, since it seems to imply an identity between the former which is a psychical matter, and the latter which is a physical matter; whereas, the one thing we may be sure about is that the psychical thing, though it is a sign and token of, is wholly different from the physical thing.

It will be as well perhaps thus early to call attention to the fact that, as indeed is shewn in Fig. 146, the image on the retina is an inverted one. What is the upper part of the object in the external world is represented in the lower part of the retinal image, what is on the right-hand side of the object is represented on the left-hand side of the image. But we are not directly conscious of this inversion of the retinal image in our own eye; we learn the fact in other ways. In the affection of consciousness to which an object seen gives rise, the inversion of the retinal image is not, in itself, felt; we take the whole complex sensation as a token or sign of the object seen, and in this we take the left-hand side, or the bottom of the retinal image, as a token or sign of the right-hand side, or the top of the object. We shall return to this matter later on; but in studying the dioptrics of the eye this inversion of the retinal image must always be borne in mind.

## SEC. 2. THE FACTS OF ACCOMMODATION.

§ **708**. When an object emitting or reflecting light, a lens, and a screen to receive the image of the object, are so arranged in reference to each other, that the image upon the screen is sharp and distinct, the rays of light proceeding from each luminous point of the object are brought into focus on the screen in a point of the image corresponding to the point of the object. If the object be then removed farther away from the lens, the rays proceeding in a pencil from each luminous point will be brought to a focus at a point in front of the screen, and, subsequently diverging, will fall upon the screen as a circular patch composed of a series of circles, the so-called *diffusion circles*, arranged concentrically round the principal ray of the pencil. If the object be removed, not farther, but nearer the lens, the pencil of rays will meet the screen before they have been brought to focus in a point, and consequently will in this case also give rise to diffusion circles. When an object is placed before the eye, so that the image falls into exact focus on the retina, and the pencils of rays proceeding from each luminous point of the object are brought into focus in points on the retina, the sensation called forth is that of a distinct image. When on the contrary the object is too far away, so that the focus lies in front of the retina, or too near, so that the focus lies behind the retina, and the pencils fall on the retina not as points, but as systems of diffusion circles, the sensation produced is that of an indistinct and blurred image. In order that objects both near and distant may be seen with equal distinctness by the same dioptric apparatus, the focal arrangements of the apparatus must be *accommodated* or adjusted to the distance of the object, either by changing the refractive power of the lens, or by altering the distance between the lens and the screen.

That the eye does possess such a power of accommodation or adjustment is shewn by every-day experience. If two needles be fixed upright, some two feet or so apart, into a long piece of wood, and the wood be held before the eye, so that the needles are nearly in a line, it will be found that if attention be directed to the far needle, the near one appears blurred and indistinct, and that, conversely, when the near one is distinct, the far one appears blurred. By an effort of the will we can at pleasure make either the far one or the near one distinct; but not both at the same time. When the eye is arranged so that the far needle appears distinct, the image of that needle falls exactly on the retina, and each pencil from each luminous point of the needle unites in a point upon the retina; but when the far needle is seen distinctly, the focus of the near needle lies *behind* the retina, and each pencil from each luminous point of this needle falls upon the retina in a series of diffusion circles; hence the image of the near needle is blurred. Similarly, when the eye is arranged so that the near needle is distinct, the image of that needle falls upon the retina in such a way, that each pencil of rays from each luminous point of the needle unites in a point on the retina, while each pencil from each luminous point of the far needle unites at a point *in front of* the retina, and then diverging again falls on the retina in a series of diffusion circles, and the far needle is now seen indistinctly. If the near needle be gradually brought nearer and nearer to the eye, it will be found that greater and greater effort is required to see it distinctly, and at last a point is reached at which no effort can make the image of the needle appear anything but blurred. The distance of this point from the eye marks *the near limit of accommodation* for near objects. Similarly, if the person be short-sighted, the far needle may be moved away from the eye, until a point is reached at which it ceases to be seen distinctly, and appears blurred; the *far limit of accommodation* is reached. In the one case, the eye, with all its power, is unable to bring the image of the needle sufficiently forward to fall on the retina: the focus lies permanently behind the retina. In the other, the eye cannot bring the image sufficiently backward to fall on the retina: the focus lies permanently in front of the retina. In both cases the pencils of rays from the needles strike the retina in diffusion circles.

§ **709.** The same phenomena may be shewn with greater nicety by what is called Scheiner's Experiment. If two smooth holes be pricked in a card, at a distance from each other less than the diameter of the pupil, and the card be held up, with the holes horizontal before one eye, the other being closed, and a needle placed vertically be looked at through the holes, the following facts may be observed. When attention is directed to the needle itself, the image of the needle appears single. Whenever the gaze is directed to a more distant object, so that the eye is no longer accommodated for the needle, the image of the needle appears double and at the same time blurred. It also appears double and blurred when the eye is accommodated for a distance nearer than that of the needle. When only one needle is seen, and the eye therefore is properly accommodated for the distance of the needle, the only effect produced by blocking up one hole of the card is that the needle and indeed the whole field of vision seems dimmer. When, however, the image is double on account of the eye being accommodated for a distance greater than that of the needle, blocking the left-hand hole causes a disappearance of the right-hand or opposite image, and blocking the right-hand hole causes the left-hand image to disappear. When the eye is accommodated for a distance nearer than that of the needle, blocking either hole causes the image on the same side to vanish. The following diagram will explain how these results are brought about.

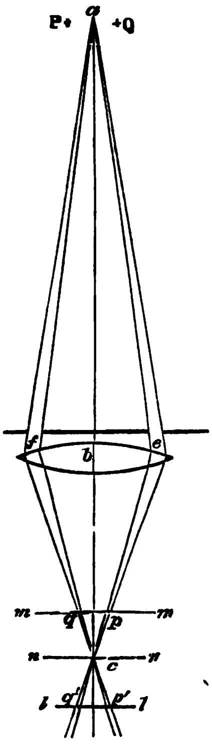

FIG. 147. DIAGRAM OF SCHEINER'S EXPERIMENT.

Let *a* (Fig. 147) be a luminous point in the needle, and *ae*, *af* the extreme right-hand and left-hand rays of the pencil of rays proceeding from the luminous point, and passing respectively through the right-hand *e*, and left-hand *f*, holes in the card. (The figure is supposed to be a horizontal section of the eye, and *a* forms part of a transverse section of the vertically placed needle.) When the eye is accommodated for *a*, the rays *e* and *f* meet together in the point *c*, the retina occupying the position of the plane *nn*; the luminous point appears as one point, and the needle will appear as one needle. When the eye is accommodated for a distance beyond *a*, the retina may be considered to lie[1] no longer at *nn*, but nearer the lens, at *mm* for example; the rays *ae* will cut this plane at *p*, and the rays *af* at *q*; hence the luminous point will no longer appear single, but will be seen as two points, or rather as two systems of diffusion circles, and the single needle will appear as two blurred needles. The rays passing through the right-hand hole *e*, will cut the retina at *p*, *i.e.* on the right-hand side of the optic axis; but, as we have already (§ 707) said, the image on the right-hand side of the retina is referred by the mind to an object on the left-hand side of the person; hence the affection of the retina at *p*, produced by the rays *ae* falling on it there, gives rise to an image of the spot *a* at *P*, and similarly the left-hand spot *q* corresponds to the right-hand *Q*. Blocking the left-hand hole, therefore, causes a disappearance of the right-hand image, and *vice versâ*. Similarly when the eye is accommodated for a distance nearer than the needle, the retina may be supposed to be removed to *ll*, and the right-hand *ae* and left-hand *af* rays, after uniting at *c*, will diverge again and strike the retina in diffusion circles at $p'$ and $q'$. The blocking of the hole *e* will now cause the disappearance of the image $q'$ on the left-hand side of the retina, and this will be referred by the mind to the right-hand side, so that *Q* will seem to vanish.

If the needle be brought gradually nearer and nearer to the eye, a point will be reached within which the image is always double. This point marks with considerable exactitude the near limit of accommodation. With short-sighted persons, if the needle be removed farther and farther away, a point is reached beyond which the image is always double; this marks the far limit of accommodation.

The experiment may also be performed with the needle placed horizontally, in which case the holes in the card should be vertical.

The determination of the accommodation of the eye for near or far distances may be assisted by using two needles, one near and one far. In this case one needle should be vertical, and the other horizontal, and the card turned round so that the holes lie horizontally or vertically according to whether the vertical or horizontal needle is being made to appear double.

§ **710**. In what may be regarded as the normal eye, the so-called *emmetropic* eye, the near limit of accommodation is about 10 or 12 cm., and the far limit may be put for practical purposes at an infinite distance. The 'range of distinct vision' therefore for the emmetropic eye is very great. In the *myopic*, or short-sighted eye, the near limit is brought much closer (5 or 6 cm.) to the cornea; and the far limit is at a variable but not very great distance, so that the rays of light proceeding from an object not many feet away are brought to a focus in the vitreous humour instead of on the retina. The range of distinct vision is therefore in the myopic eye very limited. In the *hypermetropic*, or long-sighted eye, the rays of light coming from even an infinite distance are, in the passive state of the eye, brought to a focus beyond the retina. The near limit of accommodation is at some distance off, and a far limit of accommodation does not exist. The *presbyopic* eye, or eye of advanced years, resembles the hypermetropic eye in the near point of accommodation being at some distance, but differs from it inasmuch as the former is an essentially defective power of accommodation, whereas in the latter the power of accommodation may be good and yet, from the internal arrangements of the eye, be unable to bring the image of a near object on to the retina. When an eye becomes presbyopic, the far limit may remain the same, but since the power of accommodating for near objects is weakened or lost, the change is distinctly a reduction of the range of distinct vision. When no effort of accommodation is made, the principal posterior focus of the eye lies in the normal, emmetropic eye on the retina, in the myopic eye in front of it, and in the hypermetropic eye behind it.

---

[1] Of course, in the actual eye, as we shall see, accommodation is effected by a change in the lens, and not by an alteration in the position of the retina; but for convenience sake, we may here suppose the retina to be moved.

§ **711.** By what changes in the eye are we thus able, within the above-mentioned limitations, to see distinctly objects at different distances? In directing our attention from a far to a very near object we are conscious of a distinct effort, and feel that some change has taken place in the eye; when we turn from a very near to a far object, if we are conscious of any change in the eye, it is one of a different kind. The former is the sense of an active exertion; the latter, when it is felt, is the sense of relaxation after exertion.

Since the far limit of an emmetropic eye is at an infinite distance, no such thing as active accommodation for far distances need exist. The only change which need take place in the eye in turning from near to far objects will be a mere passive undoing of the accommodation previously made for the near object. And that no such active accommodation for far distances takes place is shewn by the following facts; the eye, when opened after being closed for some time, is found adjusted not for moderately distant but for far distant objects; when the power of the eye to accommodate is impaired or abolished, as we shall see it may be, by atropin or nervous disease, the vision of distant objects may be unaffected; and we are conscious of no effort in turning from moderately distant to far distant objects. The sense of effort often spoken of by myopic persons as being felt when they attempt to see things at or beyond the far limit of their range seems to arise from a movement of the eyelids, and not from any internal changes taking place in the eye.

What then are the changes which take place in the eye, when we accommodate for near objects? It might be thought, and indeed once was thought, that the curvature of the cornea was changed, becoming more convex, with a shorter radius of curvature, for near objects. This is disproved by the fact that accommodation takes place as usual when the eye (and head) is immersed in water. Since the refractive powers of aqueous humour and water are very nearly alike, the cornea, with its parallel surfaces, placed between these two fluids, can have little or no effect on the direction of the rays passing through it when the eye is immersed in water. Moreover we have it in our power to detect any change in the curvature of the cornea which may take place. If a luminous body such as a candle be held in front of a convex surface like the cornea an image of the body is seen reflected from the surface; and, with the body at a certain distance, the image will be of a certain size. If now the curvature of the surface be increased, if the surface be made more convex, the image will diminish in size; if the curvature of the surface be diminished the image will increase in size. Indeed by measuring carefully the changes in the size of the image we may determine the amount of change in the curvature of the surface. And accurate measurements of the dimensions of an image on the cornea have shewn that these undergo no change during accommodation, and that therefore the curvature of the cornea is not altered. Nor is there any change in the form of the bulb; for any variation in this would necessarily produce an alteration in the curvature of the cornea, and pressure on the bulb would act injuriously by rendering the retina anæmic and so less sensitive. In fact, there are only two changes of importance which can be ascertained to take place in the eye during accommodation for near objects.

One is that the pupil contracts. When we look at near objects, the pupil becomes small; when we turn to distant objects, it dilates. This however cannot have more than an indirect influence on the formation of the image; the chief use of the contraction of the pupil in accommodation for near objects is to cut off the more divergent circumferential rays of light.

The other and really efficient change is that the anterior surface of the lens becomes more convex. If a light be held before the eye, three reflected images may, with care and under proper precautions, be seen by a bystander: one (Fig. 148 A, *a*) a very bright one caused by the anterior surface of the cornea, a second less bright, *b*, by the anterior surface of the lens, and a third very dim, *c*, by the posterior surface of the lens; when the images are those of an object, such as the flame of a candle, in which a top and bottom can be recognised, the two former images are seen to be erect, but the third inverted. When the eye is accommodated for near objects, no change is observed in the first, and none, or a very insignificant one, in the third of these images; but the second, that from the anterior surface of the lens, is seen to become distinctly smaller, shewing that the surface has become more convex. When, on the contrary, vision is directed from near to far objects, the image from the anterior surface of the lens grows larger, indicating that the convexity of the surface has diminished, while no change takes place in the image from the cornea, and none, or hardly any, in that from the posterior surface of the lens. And accurate measurements of the size of the image from the anterior surface of the lens have shewn that the changes in curvature which do take place are considerable; the radius of curvature of the lens accommodated for near objects is 6 mm., for far objects 10 mm.; and this difference is sufficient to account for the power of accommodation which the eye possesses.

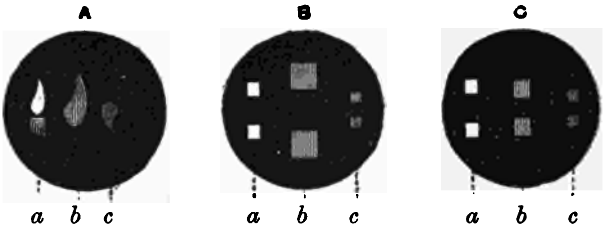

FIG. 148. DIAGRAM OF IMAGES REFLECTED FROM THE EYE.

In A are seen the three images of a candle reflected from *a*, the anterior surface of the cornea, *b*, the anterior surface of the lens, and *c* the posterior surface of the lens. *a* is bright and erect, *b*, also erect, is larger but less bright, *c* inverted is small and dim.

B shews the images, two squares, as seen in the phakoscope when the eye is directed to a far object. C the same when the eye is accommodated for a near object. The pair *b* are in C smaller and closer together than in B, shewing an increase of curvature.

The observation of these reflected images is facilitated by the simple instrument introduced by Helmholtz and called a Phakoscope. It consists of a small dark chamber, with apertures for the observed and observing eyes; a needle is fixed at a short distance in front of the former, to serve as a near object, for which accommodation has to be made; and a lamp or candle is so disposed as to throw an image on each of the three surfaces of the observed eye. Since a change in the distance between two images is more readily appreciated than is a simple change of size of a single image, two prisms are employed so as to throw a double image in the form of bright squares on each of the three surfaces, Fig. 148 B, C. When the anterior surface of the lens becomes more convex the two images reflected from that surface approach each other, C; when it becomes less convex they retire from each other, B.

These observations leave no doubt that the essential change by which accommodation is effected, is an alteration of the convexity of the anterior surface of the lens. And that the lens is the agent of accommodation, is further shewn by the fact that after removal of the lens, as in the operation for cataract, the power of accommodation is lost. In the cases which have been recorded, where eyes from which the lens had been removed seemed still to possess some accommodation, we must suppose that no real accommodation took place, but that the pupil contracted when a near object was looked at, and so assisted in making vision more distinct.

To understand, however, the mechanism by which this change in the anterior surface of the lens is brought about, we must turn to some further details of the structure of the eye.

## SEC. 3. ON THE STRUCTURE OF THE INVESTMENTS OF THE RETINA.

§ **712.** *The Sclerotic Coat.* This coat is thickest at the hind pole of the eye, where it is pierced by the optic nerve at the *lamina cribrosa,* and becomes gradually thinner forwards, though at the extreme front, close to its junction with the cornea, it is again somewhat thickened by the insertion of the ocular muscles. It consists of bundles of ordinary white fibrillated connective-tissue, with which are mingled, especially on the inner surface next to the choroid, elastic fibres and connective-tissue corpuscles, the latter frequently carrying pigment. The bundles run for the most part in two directions, longitudinally, that is meridionally, and transversely, that is equatorially; the two sets of bundles crossing each other more or less regularly at right angles. The coat as a whole therefore presents itself as a thin but tough investment, with some but not very much extensibility and elasticity.

It is somewhat scantily supplied with blood vessels, and though it contains a large number of small lymph-spaces, lined with epithelioid plates, possesses no proper lymphatic vessels. On its inside next to the choroid is a large lymphatic space, the perichoroidal space, with which the above smaller spaces communicate; and a similar large space exists on the outer surface between the sclerotic itself and an investment of looser connective-tissue called Tenon's capsule; but we shall return to these when we come to speak of the lymphatics of the whole eye.

§ **713.** *The Choroid Coat.* This, which around the optic nerve behind and at the junction of the cornea and sclerotic in front is closely attached to the sclerotic but loosely connected with it elsewhere, consists essentially of blood vessels and of certain muscular and nervous elements imbedded in connective-tissue possessing special features. It is, in the first instance, a vascular coat destined to nourish the all important retina; but muscular fibres, placed in certain parts of it, enable it to serve as a muscular mechanism as well.

The connective tissue, which forms the groundwork of the coat, has the special feature of being almost entirely destitute of white fibrillated bundles, at least in the choroid strictly so called.

It consists on the one hand of branched or irregularly polygonal corpuscles, generally loaded with pigment in the form of minute ellipsoidal crystals, and on the other hand of elastic fibres of various degrees of fineness, both elements being imbedded in a homogeneous ground substance, and for the most part arranged in lamellæ. The choroid coat therefore in contrast to the sclerotic coat is a conspicuously elastic coat.

The coat as a whole may be divided into three or more layers lying one above the other.

Immediately beneath the sclerotic the coat is loose in texture, and is made up of a series of lamellæ four or five in number, separated by lymph-spaces lined with epithelioid plates. Each lamella consists, as just described, of pigment cells and elastic fibres imbedded in a ground substance. This part of the coat, which is often called the *suprachoroidal* membrane, is separated by large irregular lymph-spaces from the inner surface of the sclerotic, which being rich in pigment cells and of somewhat looser texture than the rest of the sclerotic is sometimes distinguished as the *lamina fusca.*

Below the suprachoroidal membrane lies the layer containing the larger blood vessels, often spoken of as the choroid proper. These blood vessels are on the one hand the trunks of the ciliary arteries, short and long, with the branches into which these break up, and on the other hand the ciliary veins, which gathered up from the ciliary processes and iris as well as from the choroid itself, are arranged along the equator of the eyeball in a number of venous whorls, *the venæ vorticosæ,* the issuing veins of which pierce the sclerotic. In a vertical section through a prepared and hardened choroid these larger veins and arteries are seen cut through in various ways, the relatively small spaces between them being occupied by pigment cells and elastic fibres; towards the inner surface the fibres are especially abundant and the pigment cells scanty. The blood vessels are surrounded by perivascular lymph-spaces, and the tissue between the vessels contains numerous small lymph-spaces lined with epithelioid plates.

Beneath this layer of arteries and veins lies another layer consisting almost entirely of capillaries, into which the arteries break up and from which the veins are gathered up. This is called the *chorio-capillary membrane.* The capillary network is exceedingly close set, almost as close as that of the pulmonary alveoli; and the tissue between the vessels, reduced to a minimum, consists of a homogeneous or finely dotted ground substance in which a few branched cells, devoid of pigment, may occasionally be seen, as well as, especially in myoptic eyes, wandering leucocytes. Perivascular lymph-spaces are said to surround the capillaries.

This chorio-capillary membrane rests on a transparent homogeneous membrane, about $2\mu$ thick, called the membrane of Bruch, or *basal membrane,* which separates the choroid from the underlying pigment epithelium of the retina, and so from the retina. Although the retina possesses, as we have said, vessels of its own, these, as we shall see, are largely confined to the anterior or inner layers of the retina adjoining the vitreous humour; the posterior or outer layers of the retina, and the adjoining pigment epithelium, are nourished by the blood vessels of the choroid. Hence the great development of the chorio-capillary layer; and the rest of the choroid, if we exclude the muscular and nervous elements of which we will speak presently, serves chiefly as a means to carry blood to and from the chorio-capillary plexuses, and as a bed for the lymphatic channels rendered necessary by the amount of lymph which must be continually furnished by such a close-set capillary network.

The pigment in the choroid may be regarded as serving in addition a useful purpose, in absorbing the rays of light which have passed into it through the retina; but this cannot be of any great importance, since, as we shall see, such an absorption is chiefly carried out by the pigment epithelium of the retina.

In some animals part of the surface of the choroid when the eye is looked into shews various colours. The colouring is one not of pigments but of iridescence like the colouring of Newton's rings and thin films. It is due to the interference of light in a special layer, called the *tapetum*, intervening between the chorio-capillary membrane and the body of the choroid. In herbivora the interference of light causing iridescence is brought about by the peculiar arrangement of fine bundles of fibrillated connective-tissue; in carnivora the tapetum is composed of cells loaded with minute crystals and the interference is caused by the crystals.

**§ 714.** *The Ciliary Processes.* In front of the ora serrata, at which line the retina proper ceases, the choroid changes in character, being here thrown into the radiating plaits called the ciliary processes. These like the choroid, of which they are in fact a continuation, consist of blood vessels imbedded in a connective-tissue groundwork; but bundles of ordinary fibrillated tissue replace to a large extent the peculiar elastic lamellæ, and the capillary networks, though abundant, do not form a special close-set layer like the chorio-capillary membrane, but are more equally diffused through the bodies of the processes. The cells scattered throughout the connective-tissue bear pigment, especially in dark eyes.

The membrane of Bruch, or basal membrane, is continued over the processes, and here, often sculptured, rests on a layer of epithelium cells which do not maintain the features of the pigment epithelium of the retina, for these cease at the ora serrata, but are plain cubical cells simple in character and loaded, except in albino eyes, with black pigment. This pigment layer rests in turn on a layer of columnar cells transparent and free from pigment, into which the complex retina is suddenly transformed at the ora serrata and which as we have already said is called the pars ciliaris retinæ.

§ 715. *The Iris.* Just as the ciliary processes continue forward in a modified form the choroid coat, so the iris continues forward the same coat still further, fresh modifications being introduced; the iris is like the choroid essentially composed of blood vessels lying in a bed of connective-tissue; but it has special features of its own.

The hind surface is covered with a layer of cells loaded in all except albino eyes with black pigment. The amount of pigment is so great that the outlines of the individual cells are greatly obscured and with difficulty distinguished; but we may probably regard the cells as representing two layers, both loaded with pigment, one the continuation of the pigment epithelium of the retina and the others of the pars ciliaris retinæ. That is to say, the cells together correspond to the two layers of the retinal cup, one of which, the outer or posterior, is pigmented over the whole of the extent of the cup, while the other, the inner or anterior, is pigmented only at the back of the iris, and elsewhere forms either the pars ciliaris retinæ or the retina itself. Fig. 143. The cells cease abruptly at the margin of the pupil, which thus, as we have said, forms the extreme lip of the retinal cup.

The front surface of the iris is also covered with a layer of epithelium, resting on an inconspicuous basement membrane; but this epithelium, which is easily detached and so overlooked, consists of flat polygonal epithelioid plates, and is really a lymphatic epithelium lining the large lymphatic space called the anterior chamber.

The body of the iris between the front and hind epithelium differs somewhat in the front and back parts. The front part or anterior layer contains relatively few blood vessels, and consists chiefly of a reticular form of connective-tissue furnished by spindle-shaped branched cells mingled with elastic fibres. The hind part of the body, or, counting the pigment behind as one layer, middle or vascular layer of the whole thickness of the iris, consists largely of blood vessels which are accompanied by imperfect sheaths of ordinary connective-tissue, the intervals between the vessels being occupied by a reticular tissue like that of the anterior layer, save that the cells are more abundantly supplied with pigment. Bundles of nerve fibres, also accompanied by connective-tissue, are found in this layer but to a greater extent in the anterior layer.

Around the margin of the pupil, nearer the hind than the front surface, plain muscular fibres are gathered together in the form of a ring, the *sphincter iridis*, which compact on its inner edge towards the pupil becomes loose and frayed out on its outer edge, many of the fibres and small bundles curving away from the ring and taking a radial direction. The exact form and relative size of this sphincter muscle differs in different animals.

Resting upon the hind pigment epithelium, lying between it and the vascular layer, is a thin layer about which there has been much dispute. Seen *en face* the layer appears to consist of a number of long oval or even rod-shaped nuclei, arranged radially in a bed of material which is homogeneous save for some deposit of pigment and an obscure radiate striation. By some authors the nuclei are regarded as the nuclei of plain muscular fibres whose bodies form together the more or less homogeneous bed, and these authors accordingly speak of the layer as a radiate muscle, the *dilatator iridis*, the contractions of which would tend to widen the pupil. Other authors deny the muscular nature of this layer, and regard it as either a specially developed basement membrane, a continuation of the membrane of Bruch, or as a modified epithelial layer, the continuation of the pigment epithelium of the retina, the hind epithelium of the iris spoken of above corresponding, according to this view, to the pars ciliaris retinæ alone. We shall return to this question later on in speaking of the movements of the pupil.

§ **716**. *The Cornea.* The sclerotic coat towards the front of the eye, at about the level of the attachment of the iris, is somewhat suddenly converted from an opaque membrane into the very transparent body of the cornea. The connective-tissue instead of being arranged in a feltwork by the interlacement of meridional and equatorial bundles as in the sclerotic, is in the cornea arranged in parallel, or rather concentric, layers of bundles, all placed evenly in the same direction, the bundles of each layer and indeed the fibrillæ of the bundles being so united with cement substance that the whole is transparent. Moreover the connective-tissue corpuscles are distributed not irregularly but regularly in single layers between the layers of fibrillated material; they lie in spaces in the transparent cement substance uniting the layers together. Each cell is a broad flat thin plate with much-branched processes and a large, for the most part, oval nucleus. Since each cell lies with its broad surface parallel to the surface of the cornea and is very thin in the line of the rays of light, and since moreover the cell substance and the nucleus is, in life, transparent, the presence of these cells does not interfere with the transparency of the organ.

The front surface of the cornea is covered with an epithelium of the same nature as the epidermis of the skin (§ 433) but somewhat modified. The cells form a few layers only. The lowermost layer of vertical cells is succeeded by two or three layers of cells corresponding to those of the Malpighian layer, but irregular in form and not bearing prickles. These are in turn covered by cells, two or three deep, which become flattened towards the surface, but retain their nuclei and are not so completely transformed into horny plates as are the corresponding cells of the epidermis. The substance of each cell is sufficiently transparent to render the whole epithelium transparent. Between the epithelium and the underlying connective tissue body which corresponds to the dermis, lies a thin cuticular sheet or basement membrane, the *anterior elastic lamina* or membrane of Bowman; and from the under surface of this, prolongations in the form of fibres arch downward into the substance of the cornea.

The concave hind surface of the body of the cornea is bounded by a conspicuous cuticular membrane possessing elastic properties. This, which is sufficiently thick to give in section an easily recognised double outline, is called the *posterior elastic lamina* or *membrane of Descemet* or *of Desmours.* Upon this lies a single layer of flat polygonal epithelioid plates, which, like the similar but less conspicuous cells covering the front surface of the iris, may be regarded as the lymphatic epithelium of the anterior chamber.

In the body of the cornea neither blood vessels nor lymphatic vessels are present. At the circumference are a few capillary loops and the beginnings of a few lymphatics; but within this circle the nutrition of the cornea is effected through the branched spaces in which the corneal corpuscles lie. These, communicating freely with each other by means of their branched prolongations, and being only partially filled by the substance of the cells, form a labyrinth of lymphatic spaces, along which a flow of lymph is continually taking place. We shall deal with the nerves of the cornea in connection with those of the skin in treating of touch.

§ 717. *The Ciliary Zone.* The region in the front part of the eye at which the sclerotic changes into the cornea is of great importance, since here the choroid, represented by the outer parts of the ciliary processes and the outer margin of the iris, becomes joined to the sclerotic, and to the junction are attached the plain muscular fibres forming the ciliary muscle. This region, which we may call 'the ciliary zone,' deserves especial attention.

When the transparent body of the cornea changes into the opaque sclerotic, the epithelium of the former becomes separated from the latter by the intercalation of ordinary loose connective tissue, which serves as a dermis to the epithelium and so forms the delicate skin covering the eyeball known as the conjunctiva; the epithelium of the cornea leaves the cornea to become the epithelium or epidermis of the conjunctiva (Fig. 149 *e.cj.*). This takes place on the outside of the ciliary zone.

On the inside the curved circumferential portion of the cornea makes a blunt angle, 'iridic angle,' with the outer edge of the more or less horizontal iris; and here several peculiar structures make their appearance. The thick membrane of Descemet with its epithelioid covering is in part continued on, greatly reduced in thickness, over the front surface of the iris to form the anterior basement membrane and overlying epithelioid layer of that structure. But in part only. At the angle the compact substance of the cornea is on its inner surface frayed out into a loose network of bundles of fibres, giving rise to a number of irregular spaces, of varying sizes, the *spaces of Fontana*; and the membrane of Descemet with its epithelioid covering is also split up and frayed out to supply a cuticular and epithelioid wrapping to the bundles of the network. Thus, at the angle, a labyrinth of

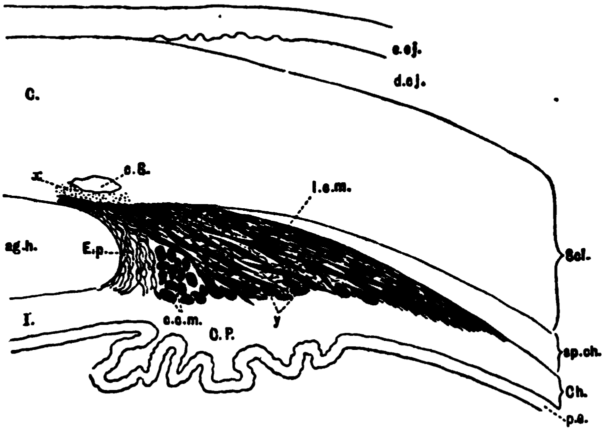

FIG. 149. DIAGRAM OF THE CILIARY MUSCLE AS SEEN IN A VERTICAL RADIAL SECTION OF THE CILIARY REGION.

*e.cj.* epithelium of the conjunctiva. *d.cj.* dermis of the conjunctiva. *Scl.* Sclerotic. *sp.ch.* suprachoroidal layer. *Ch.* Choroid. *p.e.* pars ciliaris retinae and pigment epithelium represented as one layer. *C.P.* Ciliary processes. *I.* Iris. *ag.h.* anterior chamber. *E.p.* ligamentum pectinatum. *c.S.* canal of Schlemm, and *x* tissue to inside of it.

*l.c.m.* longitudinal, and *c.c.m.* circular ciliary muscle. *y* bundles of the longitudinal muscle cut across as they are taking a circular direction.

small irregular spaces is developed continuous at many points with the large anterior chamber of the eye as well as with each other; and the bars forming the walls of these spaces consist of bundles of the corneal substance passing on to the iris, coated with a continuation of the cuticular elastic membrane of Descemet and of the epithelioid covering of that membrane. The spaces, thus continuous on the inner side with the large lymphatic space of the anterior chamber, are small lymphatic spaces communicating on the outer side with the lymphatic vessels of the choroid and sclerotic, as we shall see when we come to deal specially with the lymphatics of the eye. The system of bars defining these spaces, conspicuous through their coating provided by the elastic membrane of Descemet, are spoken of as forming the *ligamentum pectinatum* (Fig. 149 *E.p.*). They are gradually lost in the peculiar choroidal stroma of the circumference of the iris.

In a vertical section of this region a somewhat large oval space, lined by epithelioid cells, is conspicuous to the outer side of the spaces of Fontana. This is the section of a circular canal, the *canal of Schlemm* (Fig. 149 *c.S.*), which, though properly a lymphatic channel, has direct connections with neighbouring veins, and under certain circumstances becomes filled with blood.

§ **718**. *The Ciliary Muscle.* This occupies the space behind the ligamentum pectinatum between the sclerotic on the outside, and the ciliary processes and root or attachment of the iris on the inside. Just outside the ligamentum pectinatum the circular, equatorial bundles of the sclerotic are well developed, and just to the inside of the canal of Schlemm lies a small mass of denser tissue (Fig. 149 *x*); these structures serve as a point of attachment and sort of tendon for a number of small bundles of plain muscular fibres which run thence in a radiate meridional direction backwards. These interlace with other similar bundles having a similar direction and thus constitute all round the ring of the ciliary region a flat radiate meridional muscle, the *longitudinal* or *meridional ciliary muscle* (Fig. 149 *l.c.m.*), ending eventually in the front part of the choroid.

Between this and the ciliary processes and iris is seen, at least in some eyes, a number of bundles of plain muscular fibres arranged circularly, equatorially, both ends of each bundle being attached to the loose connective-tissue forming the outer part of the ciliary processes and iris. These bundles constitute the *circular ciliary muscle*, or muscle of Müller (Fig. 149 *c.c.m.*). This is as a rule less conspicuous than the longitudinal muscle and in some animals is absent. Moreover the two muscles, longitudinal and circular, are not sharply defined from each other, many of the inner bundles of the longitudinal muscle curving round so as to take an equatorial direction (Fig. 149 *y*); and it is perhaps best to speak of the whole mass as forming one muscle, 'the ciliary muscle.'

§ **719**. *The Lens.* This, as we have said, is of epithelial origin, and at an early stage presents itself as a sac with a wall consisting of a single layer of epithelium, supported by a scanty amount of mesoblast. The cavity, often from the first potential rather than actual, is soon obliterated by the elongation and growth of the cells of the hind half, and the sac is thus transformed into a solid, more or less ellipsoidal mass in which one can distinguish an anterior part formed of short cubical and a posterior part formed of elongated epithelial cells; in a section the short anterior cells may at the edge of the mass be traced gradually lengthening into the long posterior cells.

The anterior cells remain throughout life as a single layer of cubical cells, often spoken of as the anterior epithelium of the lens. The whole of the lens except this thin layer is developed out of the posterior cells. These grow into long transparent flattened prismatic bands or fibres with a hexagonal transverse section, and with serrated edges by which each fibre locks into its neighbours.

In the course of development the fibres assume a special disposition, being arranged in concentric lamellæ like the coats of an onion, the 'fibres' being so placed in the several lamellæ as to give rise to a star-shaped figure on the back of the lens. Most of the fibres still retain an elongated nucleus indicative of their epithelial nature but in many this is lost; in the adult as in the embryonic lens the transition from the characteristic fibres of the body of the lens to the cubical cells of the anterior layer may be observed in sections.

The lens develops around itself a cuticular membrane, structureless and elastic, called the *capsule of the lens*. This is much better developed in front than behind, where it is said to be partly wanting. It furnishes a distinct envelope for the lens, and when it is ruptured the lens may be turned out, leaving the cavity of the capsule vacant.

The lens thus constituted is a transparent body, of a certain refractive power (§ 705), possessing considerable elasticity; its shape may be altered by pressure, but when the pressure is removed it regains its natural form.

The chemical nature of the lens is peculiar. The proteids which seem to form about 30 p.c. of the dry solids are of a globulin nature, being apparently nearly allied to the vitellin found in yolk of eggs and elsewhere; albumin seems to be absent. Even in healthy lenses a certain variable amount of cholesterin is present, and in lenses which have become opaque, forming cataracts, especially in what are called soft cataracts, this substance occurs in considerable quantity; it may amount to 5 p.c. of the dry solids.

§ **720.** *The Vitreous Humour and Suspensory Ligament.* As we have said (§ 703), the mesoblast which is carried into the retinal cup at the involution of the lens is at first developed into the vascular pupillary and capsulo-pupillary membranes, which are supplied with blood by a continuation forwards of the central artery of the retina (Fig. 143). In the adult eye these membranes have been wholly absorbed, and the continuation of the central artery obliterated, so that all that remains of the mesoblast filling up the retinal cup is the jelly-like material known as the *vitreous humour*. This consists of little more than water, containing in solution, like the aqueous humour, about ·1 p.c. of proteids, namely, serum-albumin and globulin, as well as organic and inorganic salts; it seems chemically to resemble aqueous humour in spite of its different origin. A few scattered branched cells as well as wandering leucocytes are found in it.

Where it is in contact with the retina, the vitreous humour is defined by a structureless membrane, the *hyaloid membrane*, which is adherent normally to the overlying retina. At the ora serrata this hyaloid membrane splits into two layers, one of which is continued forward as an anterior covering for the vitreous, while the other forms an independent, faintly fibrillated, inelastic membrane, *the suspensory ligament* (Fig. 143), which is attached to and becomes fused with the capsule of the lens on the anterior surface of that body. This membrane adheres closely to the pars ciliaris retinæ for some distance, and, according to some observers, arises from the cells of this region, and is not a continuation of the hyaloid membrane.

During life the vitreous humour is in contact not only with the posterior surface of the lens, but also with the back surface of the suspensory ligament. After death, however, through changes in the vitreous humour, a space is developed, of a triangular form in section, between the suspensory ligament in front, the lens on the inside, and the vitreous humour behind; this is often spoken of as the canal of Petit. According to some authors this canal exists during life and possesses a hind wall which is furnished by the anterior continuation of the hyaloid membrane defining the front of the vitreous humour; if, as asserted, the capsule of the lens be imperfect behind (§ 719), something of the nature of a membrane must exist in the front of the vitreous humour, since, when the lens is, in extraction of cataract, removed from the capsule, the vitreous humour does not escape into the vacant cavity. Since the suspensory ligament is attached on the outside, alternately to a projecting ciliary fold and to the depression between that and the next fold, the canal of Petit, when distended with air by blowing into it, has a beaded appearance. When the canal is thus blown out the suspensory ligament and its attachments are rendered very obvious; the ring thus formed by the suspensory ligament around the lens is sometimes called the zonule of Zinn.

We shall deal with the aqueous humour in speaking of the lymphatics of the eye.

## SEC. 4. THE MECHANISM OF ACCOMMODATION AND THE MOVEMENTS OF THE PUPIL.

**§ 721.** We have seen (§ 711) that the essential change in the eye during accommodation for near objects is an increase in the curvature of the anterior surface of the lens. How is this brought about?

It has been supposed to be due to a compression of the circumférence of the lens by a contraction of the sphincter muscle of the iris, which, as we shall see, is the cause of the narrowing of the pupil attendant upon accommodation for near objects; but this is disproved by the fact that normal accommodation may take place in eyes from which the iris is congenitally absent or has been wholly removed by operation. It has also been attributed to vaso-motor changes, to increased fulness of the vessels of the iris or ciliary processes, surrounding and pressing upon the lens; but this also is disproved, not only by the fact just mentioned but as well by the fact that accommodation may be effected, after death, in an eye which is practically bloodless, by stimulating the ciliary ganglion or short ciliary nerves with an interrupted current or by other means; as we shall see, these nerves govern the accommodation mechanism. The real nature of the mechanism seems to be as follows:

The lens, as we have said, is a body of considerable elasticity. When the curvature of the anterior surface of the lens is determined, as may be done by appropriate means (by measurements of images seen by reflection from it), in its natural position in the eye at rest, and then again determined, after the lens has been removed from the eye, the anterior surface is found to be more convex in the latter than in the former case. There seems to be in the eye in its natural condition at rest some agency at work, keeping the anterior surface of the lens somewhat flattened. All that is needed is some means of counteracting this agency, and thereby allowing the lens through its elasticity to assume its natural form. And the arrangements of the suspensory ligament described in a previous section afford an explanation of what is the agency in question, and how it is counteracted.

The cavity of the eyeball behind the suspensory ligament is filled with the vitreous humour. If this is sufficiently abundant it will distend the cavity and render the suspensory ligament tense. But since the suspensory ligament passes obliquely forwards, all round, from the ciliary processes to the front of the lens, tension of the ligament will tend to flatten the lens, altering its shape but not its bulk.

The choroid, of which, as we have seen, the ciliary processes form the forward continuation, is loosely attached to the sclerotic along the line of the lamina fusca and suprachoroideal membrane; the one can to a certain extent be slipped backwards and forwards beneath the other.

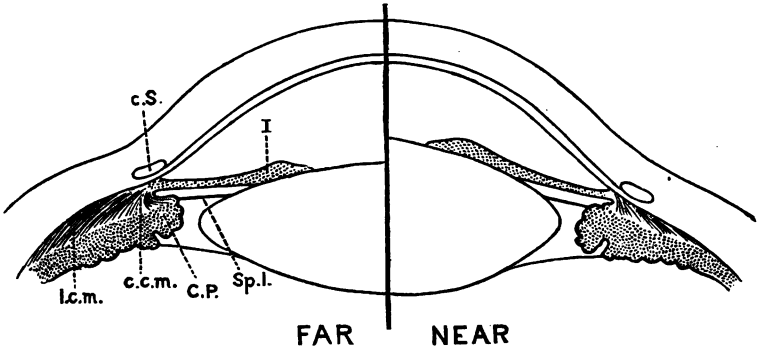

Fig. 150. Diagram to illustrate Accommodation. (After Helmholtz.)

*C.P.* Ciliary process. *I.* Iris. *Sp.l.* suspensory ligament. *l.c.m.* longitudinal ciliary muscle. *c.c.m.* circular ciliary muscle. *c.S.* canal of Schlemm.

The left half represents the arrangement for viewing far objects, and the right half that for viewing near objects.

The (longitudinal) ciliary muscle is, as we have seen, attached on the one hand to the junction of the sclerotic and cornea, and on the other hand to the front part of the choroid. If we suppose the former to be a fixed point, the contraction of the muscle would pull the moveable choroid and ciliary processes somewhat forward. But the pulling forward of these structures would slacken the suspensory ligament by bringing its ciliary attachment more forward. And a slackening of the suspensory ligament by relieving the pressure on the elastic lens would allow the front surface to become more convex. This is shewn diagrammatically in Fig. 150, one-half of which, the left half, is intended to represent the eye directed towards distant objects, while the other half represents the change taking place during accommodation for a nearer object.

§ **722.** It seems possible then that accommodation for near objects may be brought about by a contraction of the (longitudinal) ciliary muscle dragging forwards the choroid and ciliary processes, thus slackening the suspensory ligament, and so permitting the compressed elastic lens to bulge forward. And experimental evidence shews that this is what does take place. The ciliary muscle is governed, as we shall presently see, by the ciliary nerves. If in a living animal (dog) or in an eye immediately after removal from the body, an opening be made in the sclerotic in order to watch the choroid, it may be seen that when the ciliary nerves are stimulated the choroid does move forward at the same time that the front surface of the lens becomes more convex; a needle, the point of which is carefully lodged in the choroid, moves in such a way as to shew that the choroid moves forward, though no appreciable movement can be seen in a needle thrust into the front part of the ciliary muscle itself. If the cornea be cut away so as to leave only at one place a small fragment still connected to the junction of the sclerotic and cornea, this piece moves backward when the ciliary nerves are stimulated, shewing that the ciliary muscle does pull on the point of junction of the sclerotic with the cornea. When, however, the cornea is intact, or even when a sufficiently large part of it is left, the junction becomes a fixed point, at least relatively to the moveable choroid. Moreover, not only the contraction of the ciliary muscle and movement of the choroid, but the actual slackening of the suspensory ligament and change in the curvature of the lens may be observed to follow upon stimulation of the ciliary nerves. There are also observations on the human eye which shew that the suspensory ligament becomes slack during accommodation. During marked accommodation, it has been found that the lens is mobile, shaking with every movement of the head and undergoing slight displacements in various directions according to the position of the head, the direction in all cases depending on the influence of gravity. This mobility can only be explained by slackening of the suspensory ligament.

On the other hand, however, some observers have found that the anterior surface of the lens does not increase uniformly in convexity during accommodation. It is stated that the decrease of the radius of curvature from 10 mm. to 6 mm. (§ 711) is only true of the central portion, and that in the peripheral parts of the lens the change is not so great, while at the extreme periphery it is said that the lens may even become flatter during accommodation. If these observations are correct, it would be difficult to explain them by simple relaxation of the tension exerted on the anterior lens surface. The explanation given above is however probably true in the case of man and other mammals; and in favour of this conclusion is the fact that, in its main feature, the explanation has been found to hold good for birds and most reptiles. In these it has been definitely shewn that the lens becomes more convex during accommodation by a relaxation of tension, and that this relaxation of tension is brought about by contraction of a special part of the ciliary muscle which is highly developed in these animals. The actual mechanism in birds however differs in several important respects from that of man. The ciliary muscle has its more fixed attachment posteriorly, and by its contraction pulls back the inner posterior layers of the cornea, and in so doing relaxes the ligamentum pectinatum which in the state of rest is tense. In most reptiles the mechanism of accommodation resembles that of birds; but in snakes, and also in amphibia, accommodation has been found to depend on a bodily movement of the lens forward. On the other hand, it has been shewn that the eyes of fishes and cephalopods when in a state of rest are normally adjusted for near vision, and that accommodation for distance takes place by a bodily movement of the lens backward.

One or two additional points are worth mentioning. During accommodation for near objects the pupil is narrowed; we shall speak of this presently. A narrowing of the pupil means that the edge and inner part of the iris moves over the front surface of the lens towards the centre of the pupil. In becoming more convex, the front surface of the lens, especially the central portion, projects further forward into the anterior chamber, and in so doing carries with it the pupillary edge and inner part of the iris; for the iris lies close upon and indeed in contact with the anterior surface of the lens. And when the eye is carefully watched sideways this projection forwards of the pupillary margin of the iris may be observed. While the edge of the pupil thus moves forward, and the body of the iris increases in a radial direction, becoming correspondingly thinner (cf. Fig. 150), the circumferential edge of the iris is carried slightly backwards, owing to the giving way to a certain extent of the elastic ligamentum pectinatum on which the ciliary muscle pulls; and thus additional space is afforded in the anterior chamber for the aqueous humour driven aside by the projection of the anterior surface of the lens.

The action of the circular, equatorial fibres of the ciliary muscle, and of the fibres intermediate between these and the longitudinal meridional fibres, is not quite so clear. We may, however, suppose that the circular fibres acting in concert with the longitudinal fibres would bring the ciliary processes nearer to the lens, and so assist in slackening the suspensory ligament. But no very decisive explanation has been given why the circular fibres are often largely developed in some eyes, it is said hypermetropic or long-sighted eyes, and scantily present in others, myopic or short-sighted eyes. And indeed there are several points in the whole action of accommodation which still require to be cleared up.

Accommodation is in a certain sense a voluntary act; we can by looking at near or far objects bring about the change whenever we please. Since, however, the change in the lens is always accompanied by movements in the iris, it will be convenient to consider the latter before we speak of the nervous mechanism of the former.

### *The Movements of the Pupil.*

§ **723**. Although by looking at near or far objects, and so voluntarily bringing about changes in the accommodation mechanism, we can call forth the accompanying changes in the iris, and can thus at pleasure produce a constriction, narrowing, or a dilation, widening, of the pupil, it is not in our power to bring the will to act directly on the iris by itself. This fact alone indicates that the nervous mechanism of the pupil is of a special character, and such indeed we find it to be.

The pupil is *constricted*, contracted, narrowed, (1) when the retina (or optic nerve) is stimulated, as when light falls on the retina, the brighter the light the greater being the contraction; (2) when we accommodate for near objects. The pupil is also constricted when the eyeball is turned inwards, when the aqueous humour is deficient, in the early stages of poisoning by chloroform, alcohol, and similar substances, in nearly all stages of poisoning by morphia, physostigmin, and some other drugs, in the early part of the day, in deep slumber, in the epileptic seizure, and in certain nervous diseases. The pupil is *dilated*, widened, (1) when stimulation of the retina (or optic nerve) is diminished or arrested, as in passing from a bright into a dim light or into darkness, (2) when the eye is adjusted for far objects. Dilation also occurs when there is an excess of aqueous humour distending the anterior chamber, during dyspnœa, during violent muscular efforts, as the result of stimulation of sensory nerves, as an effect of emotions, as an effect of fatigue, in the later stages of poisoning by chloroform, alcohol and similar substances, in all stages of poisoning by atropin and some other drugs, and in certain nervous diseases.

§ **724**. Constriction of the pupil is caused by contraction of the circularly disposed muscular fibres which form within the iris the sphincter muscle (§ 715). The more or less spongy body of the iris being extensible, the shortening of the fibres and bundles of fibres of the sphincter must necessarily narrow the ring of the pupil of which the sphincter forms the almost immediate margin. Conversely, the body of the iris being elastic as well as extensible, a relaxation of the muscular fibres of the sphincter will lead to a widening of the pupil. We may therefore in the first instance at all events consider the constricted pupil as the result of a contraction of the sphincter muscle, and the dilated pupil as the result of a diminution of that contraction; whether the dilated pupil is merely a negative result, whether it is simply due to a lessening of the activity of the sphincter, or whether there is in addition an active dilator muscle, we will discuss later on.

We may here, however, remark that, considering how vascular the iris is, it does not seem unreasonable to interpret some of the variations in the condition of the pupil as the results of simple vascular turgescence or depletion brought about by vaso-motor action or otherwise. When the blood vessels are dilated and filled they will cause the iris to encroach on the pupil, making the latter small and narrow, and conversely a constricted and emptied condition of the blood vessels would lead to the pupil being large and wide. And indeed slight oscillations of the pupil, due to greater or less fulness of the blood vessels, may be observed synchronous with the heart-beat, and others synchronous with the respiratory movements. But the variations in the pupil are, as a rule, too marked to be merely the effects of vascular changes; and indeed that turgescence of the vessels of the iris is not the only cause of constriction of the pupil, nor depletion the only cause of dilation, is shewn by the facts that both these events may be witnessed in a perfectly bloodless eye, and that the movements of the pupil when brought about by agents which also affect the blood vessels begin some time before the changes in the calibre of the blood vessels begin, and indeed may be over and past before these have arrived at their maximum. Again, marked dilation of the pupil may be brought about by atropin without any constriction of the blood vessels. And there are other facts also shewing that the main changes of the pupil in the direction of narrowing and widening are brought about by means of plain muscular fibres in the iris apart from those of the blood vessels.

§ **725.** Of all conditions affecting the size of the pupil, the one most important and most frequently at work is the falling of light on the retina; and to this we may now turn. But before doing so it will be desirable to recall to mind the nervous supply of the eyeball, omitting for the present the nerves governing the six ocular muscles which move the eyeball as a whole.

The eyeball is supplied, in the first place, by the short ciliary nerves (Fig. 151 *s.c.*) coming from the ophthalmic or lenticular, or ciliary ganglion (*l.c.*), which is connected by means of its three roots, (1) through the so-called 'short root' with the third nerve (*r.b.*), (2) with the cavernous sympathetic plexus and so, along the internal carotid artery, with the cervical sympathetic nerve (*sym.*), and (3) through the so-called 'long root' with the nasal branch of the ophthalmic division of the fifth nerve (*r.l.*). Besides the short ciliary nerves, the eyeball is supplied by the long ciliary nerves (*l.c.*) coming direct from the nasal branch of the ophthalmic division of the fifth nerve. The short ciliary nerves, which are the most numerous, pierce the sclerotic at the hind part of the eyeball and are distributed on the one hand to the blood vessels of the choroid, ciliary processes and iris, and on the other hand to the ciliary muscle and to the sphincter of the pupil. The less numerous long ciliary nerves, piercing the sclerotic somewhat nearer the front of the eye, are distributed to the muscles of the iris, and probably to the ciliary muscle.

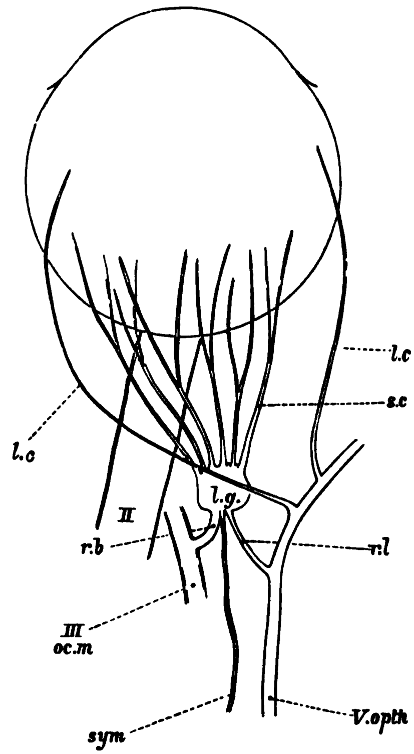

Fig. 151. Diagrammatic representation of the Nerves governing the Pupil.

*II.* Optic nerve. *l.g.* ciliary ganglion. *r.b.* its short root from *III. oc.m.*, third or oculo-motor nerve. *sym.* its sympathetic root. *r.l.* its long root from *V. ophthm.* the nasal branch of the ophthalmic division of the fifth nerve. *s.c.* the short ciliary nerves from the lenticular ganglion. *l.c.* the long ciliary nerves from the nasal branch of the ophthalmic division of the fifth nerve.

The third or oculo-motor nerve we may trace back, as we have seen (§ 623), to its nucleus in the floor of the aqueduct; the sympathetic root we may trace back along the cervical sympathetic to the spinal connections of that nerve, on which we have so often dwelt; the remarkable ophthalmic division of the fifth nerve we may trace back to the nucleus of the fifth nerve, which we have seen (§ 621) to be exceedingly complex, and indeed we have reason to consider this ophthalmic division as an independent nerve, which in the course of evolution has become annexed to other nerves to form what we call 'the fifth' nerve.

§ **726**. We may now make the broad statement, qualifications of which we will consider later on, that constriction of the pupil, brought about by light falling on the retina, is a reflex act, of which the optic is the afferent nerve, the third or oculo-motor the efferent nerve, and the centre some portion of the brain lying in the front part of the floor of the aqueduct at the level of the anterior corpora quadrigemina. This is shewn by the following facts. When the optic nerve is divided, light falling on the retina of that eye no longer causes a constriction of the pupil: we are supposing that the observations are confined to one eye. When the third nerve is divided, stimulation of the retina or of the optic nerve no longer causes constriction; but direct stimulation of the peripheral portion of the divided third nerve causes constriction of the pupil which may be extreme. If the region of the brain spoken of above as the centre be carefully stimulated, constriction of the pupil will take place even when no light falls on the retina or after the optic nerve has been divided. After destruction of the same region stimulation of the retina is ineffectual in narrowing the pupil. But if the centre and its connections with the optic nerve and third nerve be left intact and in thoroughly sound condition, constriction of the pupil will occur as a result of light falling on the retina, though all other parts of the brain be removed.

It might be imagined that this cerebral centre acted as a tonic centre, whose action was simply increased, not originated, by the stimulation of the retina; but this is disproved by the fact that if (still dealing with one eye) the optic nerve be divided subsequent section of the third nerve produces no further dilation.

When the rootlets of the third nerve are separately divided as they leave the brain, it is found that section of those placed more anteriorly interferes with accommodation and constriction of the pupil, while section of the hinder ones affects the ocular muscles. Moreover if the hind part of the floor of the third ventricle and front part of the floor of the aqueduct be carefully explored (in the dog) by means of the interrupted current, the following movements may be observed in succession as the electrodes are shifted from the front backwards; first movements of accommodation, next constriction of the pupil, and then contractions of the ocular muscles. Now in this region lies the elongated nucleus of the third nerve (§ 623); and it would appear that while the fibres of the third nerve concerned in accommodation arise from the extreme front of the nucleus, those which act upon the pupil start from a succeeding part, the remaining hinder part giving rise to the fibres which govern the ocular muscles. It seems therefore natural to regard the part of the nucleus from which the pupil-constricting fibres spring, as the centre of the reflex pupil-constricting mechanism, as the pupil-constrictor centre.

There is no difficulty as to the connection of the centre with the efferent limb of the reflex chain. The pupil-constrictor fibres pass from the nucleus to the trunk of the third nerve of the same side, and so by the short root to the ciliary ganglion (Fig. 151 *r.b.*), whence they reach the pupil by the short ciliary nerves; section of the short ciliary nerves breaks the reflex chain of which we are speaking, and stimulation of them or of their peripheral ends causes narrowing of the pupil.

The determination of the afferent path has been a matter of considerable difficulty but there is now little doubt that there are in the optic nerve special fibres smaller than those which have to do with visual sensations which form the afferent part of the pupil reflex. These fibres are at first mingled with the visual fibres but near the corpora quadrigemina they collect into a bundle which emerges from the upper median edge of the optic tract and enters the roof of the anterior corpus quadrigeminum. From this situation the fibres pass downwards to one of the groups of small cells which form part of the oculo-motor nucleus (§ 623).

It is desirable to remember one important difference as to the behaviour of the pupil which obtains between man and some of the higher mammals on the one hand, and the lower mammals as well as other vertebrates on the other. In the former, the pupil-constricting nervous mechanisms of the two eyes are not completely independent; there is a functional communion between the two sides, so that when one retina is stimulated both pupils contract, and indeed, in man, as a rule, contract equally. Hence, when a change in the pupil of one eye is brought about by some means other than the one we are now considering, the pupil of the other eye is affected; when for instance one pupil is dilated with atropin, the larger amount of light thus admitted into that eye causes a narrowing of the pupil of the other eye, and thus increases the difference between the pupils of the two eyes. In the lower mammals and other vertebrates, the mechanisms in question are independent, stimulation of one retina produces no effect on the pupil of the other eye. This difference seems to be dependent on the character of the optic decussation which, as we have seen, (§ 667) is connected with the presence or absence of binocular vision. In man, with highly developed binocular vision, the decussation is partial (Fig. 141) and corresponding to this partial decussation of the visual fibres, there is also a partial decussation of the pupil fibres. When one optic tract is divided or diseased, the hemianopia so caused is accompanied by a hemiopic pupil reflex; stimulation of the blind half of each retina by light fails to elicit reflex constriction of the pupil.

Whatever be the exact nature of the central connections, the existence of the reflex constrictor mechanism is an important fact, since the changes of the pupil which take place in actual life are to a large extent carried out by means of it; a constricted pupil indicates in the majority of instances an activity of the reflex mechanism, and a dilated pupil the absence of or diminution of that activity. In the normal, healthy organism the activity of the mechanism is in the first instance dependent on the amount of light falling on the retina; but even in the normal condition, and still more in an abnormal condition of the organism, other influences may become dominant. The activity of the centre may be exalted or depressed by nervous or other actions; the retina or optic nerves may be affected by the same amount of light to a degree less than or greater than the normal, and the efferent limb of the chain may be less or more effective.

§ **727.** Besides, however, all the various changes which may thus be induced by playing upon the optic-oculo-motor reflex mechanism, there are other agencies capable of acting on the pupil quite apart from this reflex mechanism.

If the cervical sympathetic in the neck be divided, all other influences which could possibly affect the pupil being avoided, a constriction of the pupil will be seen to take place; this however is at times (in animals) not very well marked; but, whether it be so or no, if the peripheral portion of the nerve (*i.e.* the upper portion still connected with the head) be stimulated, a well-developed dilation is the result. The cervical sympathetic has, it will be observed, an effect on the pupil, the opposite of that which it exercises on the blood vessels of the head and neck; when it is divided, the pupil becomes constricted but the blood vessels dilate, and when it is stimulated the pupil is dilated while the blood vessels are constricted. This pupil-dilating influence of the cervical sympathetic may, as in the case of the vaso-constrictor action of the same nerve, be traced backwards down the neck along one or other or both the limbs of the annulus of Vieussens to the upper thoracic (stellate) ganglion. From thence it may be traced along the rami communicantes and anterior roots of certain upper thoracic nerves to the spinal cord. The exact path differs in different animals; in the dog, cat, monkey, and probably in man, the path lies chiefly in the second thoracic nerve, but also in the first, and occasionally in the third; in the rabbit it is chiefly in the second and third; and in the frog it is the fourth spinal nerve. Along the spinal cord the dilating influence may be further traced upwards through the bulb to a centre, which appears to be placed in the floor of the front part of the aqueduct not far from and apparently lateral to the centre for constriction of the pupil. Since, as a rule, a very decided amount of narrowing of the pupils follows upon mere section of the cervical sympathetic, we may infer that, unlike the case of the pupil-constrictor mechanism, tonic impulses habitually proceed from the pupil-dilator centre.

We may trace the path of dilating impulses in the other direction upwards along the cervical sympathetic, not to the sympathetic root of the ciliary ganglion and so to the short ciliary nerves, but to fibres which, passing over the Gasserian ganglion apply themselves to the ophthalmic division of the fifth nerve, and from thence along the nasal branch to the long ciliary nerves, and so to the iris; while the short ciliary nerves are the channels for pupil-constrictor impulses, the long ciliary nerves are the channels of pupil-dilator impulses.

§ **728**. But while the mode of action of the pupil-constrictor impulses seems clear, since these have simply to throw into contraction, or increase the contraction of, the fibres of the sphincter, the mode of action of the pupil-dilator impulses is a matter which has been and still is disputed. We have already (§ 724) urged that the widening of the pupil cannot be simply the result of vaso-constrictor action on the blood vessels of the iris.

But even admitting that the widening is the direct effect of changes in contractile tissue, two views may still be urged. Did there exist in all eyes obvious strands of plain muscular tissue radially disposed, so that their contraction by pulling radially on the margin of the pupil would necessarily widen the pupil, the divergence of views would probably have never arisen; but such obvious strands are quite exceptional, occurring only in one or two kinds of mammals; and in most irises the only possible radially disposed contractile material is a layer of somewhat obscure nature lying immediately in front of the hind pigment epithelium. One view emphasizing the absence of indubitable radial muscular tissue maintains that the widening of the pupil resulting from stimulation of the sympathetic is simply the effect of an inhibition of the sphincter. It is argued that the sphincter may be compared to the heart, inasmuch as it possesses an automatic power of contraction, manifested however not in a rhythmic but in a tonic manner, and that like the heart its action may be either augmented or inhibited by nervous impulses; and we have seen (§ 429) that a similar view may be taken of the actions of the plain muscular fibres of the alimentary canal and of the bladder. According to this view the sphincter of the iris, when removed from all influences, is in a state of tonic contraction, pulling against the radiate strain of the elastic tissue of the iris and so maintaining a pupil of a certain size. Under the influence of light falling on the retina, impulses reaching the sphincter by the short ciliary nerves augment its contraction, and narrow the pupil in proportion to their intensity. On the other hand, impulses reaching the sphincter from the sympathetic by the long ciliary nerves inhibit the activity of the sphincter, diminish the force with which it is pulling against the elastic tissue of the iris, and so lead to a widening of the pupil, thus either diminishing the constriction which is being caused by the action of light on the retina or otherwise, or, in the absence of all external constricting influences, causing the pupil to become wider than it naturally would when removed from all extrinsic influences whatever. In support of such a view it is pointed out that the muscular tissue forming the sphincter is peculiar, since a slip of it when directly stimulated by a weak interrupted current elongates, in this respect also shewing its analogy with the heart whose activity may similarly be inhibited by the interrupted current. Again, in the extirpated eye, or even in the isolated iris, cold dilates and warmth constricts the pupil, the one relaxing, and the other increasing the contraction of the sphincter. On the other hand it is urged not only that stimulation of one of the long ciliary nerves, or, through the application of the electrodes to the sclerotic just behind the attachment of the iris, of the branches going to limited portions of the iris, leads to an unevenly dilated pupil but also that a radial slip of the iris, cut out from the rest of the iris, but with its circumferential attachment untouched, may be seen to contract radially when the sympathetic is stimulated, and that too when the sphincter is made to contract at the same time. These observations seem to shew that the widening of the pupil caused by stimulation of the sympathetic is due to contraction of some radially disposed contractile tissue; and the fact that this radial contraction fails if the hind surface of the iris be previously roughly brushed, strongly confirms the view that the radially disposed contractile tissue in question is the layer mentioned above as lying immediately in front of the pigment epithelium.

Whatever be the view adopted as to the exact mode of action of the sympathetic there remains the broad fact that the pupil is under the dominion of two antagonistic mechanisms: one a constricting mechanism, reflex in nature, the third nerve serving as the efferent, and the optic as the afferent tract; the other a dilating mechanism, apparently tonic in nature, but subject to augmentation from various causes, and of this the cervical sympathetic is the efferent channel. Hence, when the third or optic nerve is divided, not only do constricting impulses cease to be manifest, but the effect of their absence is increased, on account of the tonic dilating influence of the sympathetic being left free to work. When, on the other hand, the sympathetic is divided, this tonic dilating influence falls away, and constriction results. When the optic or third nerve is stimulated, the dilating effect of the sympathetic is overcome, and constriction results; and when the sympathetic is stimulated, any constricting influence of the third nerve which may be present is overcome, and dilation ensues.

The former, optic oculo-motor mechanism is the instrument by means of which the pupil is adapted to the amount of light, the latter, sympathetic mechanism appears to be employed when other influences are brought to bear on the pupil. Thus the characteristic pupil-dilating effects of emotions such as fear, of the painful stimulation of sensory nerves, of dyspnœa, and in part of some drugs, appear to be carried out through the sympathetic mechanism.

§ **729**. In the case of many drugs, however, the effect produced is either in part or wholly independent of both these nervous mechanisms. A small quantity of atropin introduced into the system, or even directly into the eye, causes a dilation of the pupil which may be so great that the iris is reduced to a mere rim, while physostigmin (eserin) similarly introduced into the system or eye produces a constriction of the pupil which may be so great that the pupil is narrowed to a mere pin's point. Since both these drugs may produce their full effects after division of the optic, oculo-motor and the sympathetic nerves, and indeed may produce their effects in an extirpated eyeball, it is obvious that those effects are not due to the drugs acting on the central parts of the above mechanisms. Their action is a local one. They do not act by means of the ciliary ganglion, for both drugs continue to produce their effects to a most marked degree after the ganglion has been excised. Nor have we any evidence that their action is dependent on any other local nervous mechanism, such as might be afforded by the nerve cells lying in the choroid or even in the iris. They appear to act directly on the sphincter, atropin paralyzing it or producing relaxation, and physostigmin increasing or producing contraction, both often of an extreme character. Whether the drugs act on the actual muscular tissue itself or on the endings of the nerve fibres in the muscular tissue, or on both together, is a question which we cannot discuss here. Nor need we stay to consider the difficulties which are added, if we accept the view of the existence of a special dilator muscle. The important point is that the action of both these drugs is a local one; hence, when they have produced their full effects, the normal nervous mechanisms on which we have been dwelling are of little or no use; even an abundance of light leads to no constriction in the full atropinized eye, and removal of light produces little or no dilation in an eye fully under the influence of physostigmin.

We may here mention the fact that in some fishes and amphibia, for instance the eel, salamander and frog, light falling into an extirpated eye will cause constriction of the pupil; and this seems to be brought about by the direct action of light on the muscular structures of the iris, for in eyes which have been made especially sensitive by being kept in the dark, the constriction of the pupil occurs when the whole posterior part of the eyeball has been destroyed. It has been suggested that special pigment granules, lying in the muscular fibres between the fibrils, act as the intermediate agent between the light and the contractile substance.

§ **730**. *The nervous mechanism of accommodation.* The ciliary muscle which brings about accommodation is governed in this action by fibres which may be traced, through the short ciliary nerves and ciliary ganglion, along the third nerve, to a centre which lies (in dogs) in the extreme front of the floor of the aqueduct, or rather perhaps in the extreme hind part of the floor of the third ventricle, and which is especially connected with the extreme front of the nucleus of, and so with the most anterior bundles of the root of, the third nerve. As we have already said stimulation of this centre, or of the third nerve, or of the short ciliary nerves, leads to a contraction of the ciliary muscle and to accommodation for near objects.

This nervous mechanism is much more directly under the control of the will than is that of the pupil but both accommodation and relaxation of accommodation may be purely reflex. The mechanism may, however, be affected by the local action of drugs. Such drugs as atropin and physostigmin which have a special action on the pupil, also affect the mechanism of accommodation. Atropin paralyses it, so that the eye remains adjusted for far objects; and physostigmin throws the eye into a condition of forced accommodation for near objects. This double action has been explained by the supposition that, by acting on the muscular fibres, or on the nerve endings, or on both, atropin inhibits the contraction of or paralyses, while physostigmin throws into contraction or augments the contraction of the ciliary muscle. But the phenomena, on further inquiry, are found to be more complicated than they appear to be at first sight, and there are other facts which indicate that our knowledge of the mechanism of accommodation is far from being complete. For instance, so far as we know at present, when we pass from accommodation for a near object to that for a far object, we simply 'let go' the previous effort; we cease to contract the ciliary muscle, and, the return of the suspensory ligament and other parts seems to be simply the passive result of the cessation of the contraction of the ciliary muscle. If now the change from near to far be such a mere passive relaxation of a previous contraction we should, judging from our experience of ordinary muscular contractions, expect the time taken up by it to be greater, or at least not less than the time taken up by the change from far to near; but as a matter of fact it is very much shorter, indeed the act is an exceedingly rapid one.

§ **731**. There remains a word to be said concerning the constriction of the pupil which takes place when the eye is accommodated for near objects, and when the pupil is turned inwards (the two being closely allied, since the two eyes converge to see near objects), and the return to the more dilated condition when the eye returns to rest and regains the condition adapted for viewing far objects. These are instances of what are called "associated movements." A similar instance is afforded by certain cases of blindness of one eye due to atrophy of the optic nerve;

in such cases the pupil of the blind eye may be wholly insensible to light, and yet becomes narrowed when the subject looks at a near object with the sound eye. In so doing he throws into action the accommodation mechanism, and with that the pupil-constricting mechanism of both eyes. Two movements are thus spoken of as "associated" when the special central nervous mechanism employed in carrying out the one act is so connected by nervous ties of some kind or other with that employed in carrying out the other, that when we set the one mechanism in action we unintentionally set the other in action also. In this constriction of the pupil associated with accommodation the nervous ties between the parts of the central nervous system concerned in the generation of the will, the centre for accommodation, and the centre for the constriction of the pupil, are such that whenever the will stirs up the impulses necessary to carry out accommodation, it at the same time stirs up corresponding impulses in the pupil-constrictor mechanism. More than this we cannot at present say.

We can, as we have said, accommodate at will; few persons only can effect the necessary change in the eye unless they direct their attention to some near or far object, as the case may be, and thus assist their will by visual sensations. By practice, however, the aid of external objects may be dispensed with; and it is when this is achieved that the pupil may seem to be made to dilate or contract at pleasure, accommodation being effected without the eye being directed to any particular object.

## SEC. 5. IMPERFECTIONS IN THE DIOPTRIC APPARATUS.

§ **732**. *Imperfections of accommodation.* The emmetropic eye, in which the principal posterior focus lies on the retina, may, as we have said, be taken as the normal eye. The myopic, in which the principal posterior focus lies in front, and the hypermetropic eye, in which it lies beyond the retina, may be considered as imperfect eyes, though the former possesses an advantage over the normal eye in so far that it can see minute objects more distinctly than can the normal eye, since these can be brought so near the eye as to give a relatively large retinal image and yet remain within the limits of accommodation. An eye may be myopic from too great a convexity of the cornea, or of the anterior surface of the lens, or from permanent spasm of the accommodation-mechanism, or from too great a length of the long axis of the eyeball. The last appears to be the usual cause. Similarly, the cause of hypermetropia is in most cases the possession of too short a bulb. In presbyopia the failure or loss of accommodation may be due either to a loss of elasticity of the lens, or to increasing weakness of the ciliary muscle, or to the parts becoming rigid; the first appears to be the more common cause; the change, which may affect not only normal but also other eyes, generally begins in the fifth decade of life.

These several defects may be remedied by the use of appropriate lenses, by wearing proper spectacles. The myopic eye needs for distant objects the rays of which fall parallel on the cornea (or at least so little divergent that they still are brought to a focus in front of the retina) a concave glass, of such a refractive power, of such a focal length, as to give to parallel rays sufficient divergence before they fall on the cornea to enable the dioptric mechanism of the eye to bring them to a focus on, and no longer in front of, the retina.

The hypermetropic eye needs a convex glass of such a focal length as will give to parallel rays sufficient convergence before they fall on the cornea to enable the eye to bring them to a focus on the retina.

The presbyopic eye similarly needs a convex glass the focal length of which must depend on the amount of accommodation still possessed by the eye; it must give the rays just so much convergence that the weakened mechanism is able to bring them to a focus on the retina, the convexity or refractive power of the glass being increased, that is to say, its focal length diminished, as the loss of accommodation increases.

§ **733**. *Spherical aberration.* In a spherical lens the rays which are refracted by the circumferential parts are brought to a focus sooner than those which pass through the more central parts; in consequence the rays proceeding from a luminous point are no longer brought to a single focus at one point, but form a number of foci at different distances. Hence, when rays are allowed to fall on the whole of the lens, the image formed on a screen placed in the focus of the more central rays is blurred by the diffusion-circles caused by the circumferential rays which have been brought to a premature focus. In an ordinary optical instrument spherical aberration is obviated by a diaphragm which shuts off the more circumferential rays. In the eye the iris is an adjustable diaphragm; and when the pupil contracts in near vision the more divergent rays proceeding from a near object, which tend to fall on the circumferential parts of the lens, are cut off. The lens however, as we have seen, is not uniform in structure, and the refraction which it exercises does not, as in the case of the ordinary lens, increase regularly and progressively from the circumference to the centre, but varies most irregularly; hence the purpose of the narrowing of the pupil cannot be simply to obviate spherical aberration; and indeed the other optical imperfections of the eye are so great, that such spherical aberrations as are actually caused by the lens produce no obvious effect on vision.

§ **734**. *Astigmatism.* We have hitherto treated the eye as if its dioptric surfaces were all parts of perfect spherical surfaces. In reality this is rarely the case, either with the lens or with the cornea. Slight deviations from the spherical shape do not produce any marked effect, but there is one deviation, known as regular astigmatism, which, present to a certain extent in most eyes and very largely developed in some, frequently leads to very imperfect vision. This defect is due to one or other of the dioptric surfaces being not spherical but more convex along one meridian than another, more convex, for instance, along the vertical than along the horizontal meridian. When this is the case with the dioptric surface of an optical system the rays proceeding from a luminous point are not brought to a single focus at a point, but possess two foci each of which is not a point but a line, a linear focus. In simple astigmatism, one of these foci is in the same situation as the normal focus, while the other linear focus may be in front of or behind it. The anterior of the two foci corresponds to the more convex, the posterior to the less convex surface. If the vertical meridians of the surface be more convex than the horizontal, then the anterior linear focus will be horizontal and the posterior linear focus will be vertical, and *vice versâ.* (This can be shewn much more effectually on a model than in a diagram, in which we are limited to two dimensions.) Now, in order to see distinctly a vertical line, it is much more important that the rays which diverge from the line in a series of horizontal planes should be brought to a focus properly than those which diverge in the vertical plane of the line itself; for the former contribute to a far greater extent than do the latter to the sum of rays which go to form the retinal image of and so to excite the sensation of the line. Similarly, in order to see a horizontal line distinctly it is much more important that the rays which diverge from the line in a series of vertical planes should be brought to a focus properly than those which diverge in the horizontal plane of the line itself. When a horizontal line is held before an astigmatic dioptric surface, more convex in the vertical meridian, it will give rise to a well-defined image of a horizontal line at the anterior focus where the many vertical rays diverging from the line are brought to a linear horizontal focus, and to a blurred image of a vertical line at the posterior focus where the fewer horizontal rays are brought to a linear vertical focus. Similarly, a vertical line held before the same surface will give rise to a well-defined image of a vertical line at the posterior focus where the horizontal rays diverging from the vertical line are brought to a linear vertical focus, and to a blurred image of a horizontal line at the anterior focus. Hence if a horizontal and a vertical line be placed at the same distance before an astigmatic eye which is more convex in the vertical meridian, that eye will see a horizontal needle distinctly when the anterior, and a vertical needle distinctly when the posterior of the two foci falls on the retina; it will require a different accommodation to see the one and the other distinctly. If the astigmatism is such that the horizontal meridian be the more convex, the vertical needle will be seen most distinctly at the anterior, and the horizontal at the posterior focus. It seems probable, however, that in ordinary vision the astigmatic eye is not adjusted for either of its linear foci. Between these linear foci there is a region in which the retinal image of a point is more or less elliptical. In an astigmatic eye with a more convex horizontal meridian, that is, with an anterior vertical focus and a posterior horizontal focus, the retinal image of a point will pass, as the eye adjusts itself, through the following successive phases: a vertical line, an ellipse with its longer axis vertical, an ellipse with its longer axis horizontal, and lastly a horizontal line. Between the two elliptical conditions there will be a point at which the image will be approximately circular, and it is probable that the astigmatic eye is usually adjusted for this approximately circular focus. A point of light would therefore be seen as a circular patch, and objects of various forms will shew a corresponding indistinctness.

Most eyes are thus more or less 'regularly' astigmatic, and generally with a greater convexity along the vertical meridian. If a set of horizontal or vertical lines be looked at, or if the near point of accommodation be determined by Scheiner's experiment, for the needle placed first horizontally and then vertically, the distance from the eye at which the horizontal lines or needle are seen distinctly will be found, in most cases, to be appreciably and in many cases considerably shorter than that at which the vertical lines or needle are seen with equal distinctness. In other words, in the case of most eyes, a vertical line must be farther from the eye than a horizontal one, if both are to be seen distinctly at the same time. The cause of astigmatism is, in the great majority of cases, the unequal curvature of the cornea; but sometimes the fault lies in the lens, as was the case with the philosopher Young.

Regular astigmatism may be remedied by the use of cylindrical glasses, that is to say, glasses which are convex along one meridian but plane along the other. Thus the ordinary astigmatic eye with the greater curvature along the vertical meridian will be benefited by a cylindrical glass, plane in the vertical plane but possessing such convexity in the horizontal plane as will make up for the relatively deficient horizontal curvature of the cornea.

When the curvature of the cornea or of the lens differs not in two meridians only but in several, *irregular* astigmatism is the result. A certain amount of irregular astigmatism, due to the cornea or lens, exists in most eyes, thus causing the image of a bright point, such as a star, to be not a round dot but a radiate figure; in some cases the irregularity is so great that several imperfect images are formed of every object.

§ **735.** *Chromatic aberration.* The different rays of the spectrum are of different refrangibility, those towards the violet end of the spectrum being brought to a focus sooner than those near the red end. This in optical instruments is obviated by using compound lenses made up of various kinds of glass. In the eye we have no evidence that the lens is so constituted as to correct this fault; still the total dispersive power of the instrument is so small, that such amount of chromatic aberration as does exist attracts little notice. Nevertheless some slight aberration may be detected by careful observation. When the spectrum is observed at some distance off the violet end will not be seen in focus at the same time as the red end. Again, if a luminous point be looked at through a narrow orifice covered by a piece of violet glass, which while shutting out the yellow and green allows the red and blue rays to pass through, there will be seen alternately an image having a blue centre with a red fringe, or a red centre with a blue fringe, according as the image of the point looked at is thrown on one side or other of the true focus. Thus supposing *f* (Fig. 152) to be the plane of the mean focus of *A*, the violet rays will be brought to a focus in the plane *V*, and the red rays in the plane *R*.

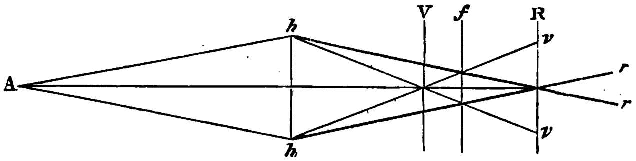

FIG. 152. DIAGRAM ILLUSTRATING CHROMATIC ABERRATION.
*hh* is the dioptric surface, *hv* represents the blue, and *hr* the red rays; *V* is the focal plane of the blue, *R* of the red rays.

If the rays be supposed to fall on the retina between *V* and *f*, the diverging or blue rays will form a centre surrounded by the still converging red rays; whereas if the rays fall on the retina between *f* and *R*, the converging red rays will form a centre with the still diverging blue rays forming a fringe round them. If the rays fall on the retina at *f*, the two kinds of rays will be mixed together; as will be seen from the figure, the circumferential still converging red ray *hr* as it cuts the plane of the retina is, in ordinary vision, accompanied by the diverging violet ray *hv*, and thus by a sort of compensation, we see together, though not in absolutely proper focus, even the rays which differ most in refraction. The experiment may be varied by blocking up one half of the pupil with a piece of card and using the uncovered half of the pupil to look through a piece of violet glass at a white surface or a candle flame. The violet strip will be seen to have a blue edge.

§ **736**. *Entoptic phenomena.* The various media of the eye are not uniformly transparent; the rays of light in passing through them undergo local absorption and refraction, and thus various shadows are thrown on the retina, of which we become conscious as imperfections in the field of vision, especially when the eye is directed to a uniformly illuminated surface. These are spoken of as entoptic phenomena, and are very varied, many forms having been described.

Tears on the cornea, or temporary unevenness of the anterior surface of the cornea after the eyelid has been pressed on it, may give rise to retinal images and so to visual sensations; but in these cases the cause lies outside the eye and the result can hardly be spoken of as entoptic.

Changes in the margin of the pupil appear in the shadow of the iris which bounds the field of vision. If we look at a bright object or luminous surface through a pin-hole in a card placed close in front of the eye (in order to get the best image on the retina, the pin-hole should occupy the position of the principal anterior focus), the dark circle which bounds the field of vision is the image caused by the shadow of the margin not as might at first be supposed of the pin-hole but of the iris. This is at once shewn by the changes which it can be made to undergo, while the pin-hole remains motionless, by alternately closing and opening the other eye; the field of vision of the eye which is looking through the pin-hole may be observed to contract when light enters, and to expand when the light is shut off from the other eye; for as we have seen (§ 726) light falling on one retina leads to consensual narrowing of the pupil of the other eye. Other changes or irregularities in the iris may be observed by this method.

Imperfections in the lens or in its capsule may also give rise to entoptic images. Not unfrequently a radiate figure corresponding to the arrangement of the fibres of the lens makes its appearance.

The most common entoptic phenomena are those caused by the presence of floating bodies in the vitreous humour, the so-called *muscæ volitantes.* These are readily seen when the eye is turned towards a uniform surface, and are frequently very troublesome in looking through a microscope. They assume the form of rows and groups of beads, of single beads, of streaks, patches and granules, and may be recognised by their almost continual movement, especially when the head or eye is moved up and down. When an attempt is made to fix the vision upon them they immediately float away.

Since the images on the retina are in these cases shadows and since the strongest shadows are cast by parallel rays, the images are best seen when the rays of light giving rise to the shadows on the retina traverse the vitreous humour in parallel lines; hence the best illumination for examining the phenomena is one placed in the principal anterior focus, the rays diverging from which fall parallel on the retina (§ 704, Fig. 144). The sharpness of the images is also increased by using a small but bright source of light, as by looking at a bright light through a small hole in a screen.

The sensations which these objects in the vitreous humour excite by means of the retinal images to which they give rise do not tell us that the objects are in the vitreous humour. As we shall see we refer all affections of the retina, all visual sensations to some changes in the external world; and if we trusted to our sensations alone in the cases of these entoptic phenomena we should suppose that the causes existed outside ourselves. It is only by means of inferences drawn from the features and behaviour of the sensations that we arrive at the conclusion that the causes lie in the vitreous humour.

The accompanying diagram (Fig. 153) illustrates how the position of objects in the eye may be determined by the movements of their shadows on the retina. It represents the reduced diagrammatic eye seen in vertical section, with *n* the nodal point, *p* the principal plane, and *F* the plane of the principal anterior

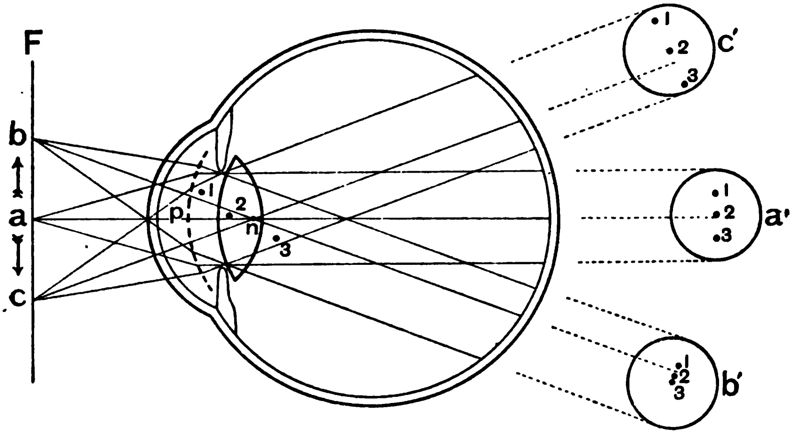

FIG. 153. DIAGRAM TO ILLUSTRATE ENTOPTICAL IMAGES.

focus. 1 represents an object in the anterior chamber, 2 another in the substance of the lens, and 3 a third in the vitreous humour. If a bright light be looked at through a pin-hole in a card placed in the plane of the principal anterior focus *F* so that the hole is at the principal anterior focus *a*, the rays of light may be considered as diverging from *a*, and we may draw them as refracted at the principal plane *p*, and then passing parallel through the vitreous humour. The image on the retina in this case may be represented by *a'*. The field of vision, limited by the shadow of the iris, will be circular; the shadow of 2 will lie close to the optic axis, that of 1 a little above it, and that of 3 some little way below it. It will of course be remembered that in the *apparent* image all the features will be inverted (§ 707). If now the card be moved upward so that the light emanates from the pin-hole at *b*, and the paths of the rays of light be drawn as before, the image resulting will be that shown at *b'*. The shadow of 2 has changed very little in position; but that of 1 has moved downwards, while that of 3 has moved upwards so that all three lie closer together. If, on the contrary, the card be moved downward to *c* the result will be that shewn in *c'*; the shadow of 2, as before, has moved but little, while that of 1 has moved upward, and that of 3 downwards, so that the three shadows are farther apart.

Thus while the shadows of objects in the anterior chamber move in a direction the opposite to that of the movement of the source of an illumination placed in the plane of the principal anterior focus, the shadows of objects in the vitreous humour move in the same direction as the source of illumination. Hence, by observing the direction of the movement of an entoptic image resulting from the movement of the illumination, the position in the eye of the object giving rise to the image may be determined, regard of course always being had to the so-called mental inversion of the retinal image. Stated more strictly the rule would run thus. The shadows of objects in front of the nodal point (§ 705) in the lens move in a direction contrary to and those of objects behind the nodal point in the same direction as the movement of the illumination; moreover the more distant the object from the nodal point the greater the movement of the shadow caused by the same movement of the illumination.

In this connection we may refer to one or two matters which however cannot be called dioptric imperfections.

If a white sheet or white cloud be looked at in daylight through a Nicol's prism, a somewhat bright double cone or double tuft, with the apices touching, of a faint blue colour, is seen in the centre of the field of vision, crossed by a similar double cone of a somewhat yellow darker colour. These are spoken of as Haidinger's brushes; they rotate as the prism is rotated, and are supposed to be due to the unequal absorption of the polarised light in that part of the retina which we shall study presently as "the yellow spot." The prism must be frequently rotated, since when the prism remains at rest the phenomena fade. We may here remark that the media of the eye are fluorescent: a condition which favours the perception of the ultraviolet rays. There are other entoptic phenomena due to features of the retina, of which we shall speak in treating of the development of visual impulses.

Lastly, returning to dioptric imperfections, we may add that the optical arrangements are also to a certain extent imperfect inasmuch as the dioptric surfaces are, according to most observers, not truly centred on the optic axis.

## SEC. 6. THE STRUCTURE OF THE RETINA.

**§ 737.** We have now to inquire how the rays of light thrown on to the retina, by means of the dioptric mechanism, in the form of an optical image give rise to visual sensations and so to a perception of the object sending forth the rays. For this purpose we must turn to the structure of the retina, including with it the pigment epithelium derived from the outer, as the retina proper is from the inner, layer of the retinal cup.

*The optic nerve,* as we have already said, is not so much an ordinary nerve as a strand of white matter extending from the brain; and several of its features shew this. Its outer wrapping is not an ordinary perineural sheath but a prolongation of dura mater, and within this lies a 'pial' sheath, a continuation of the pia mater. Between the two may be recognised a membrane corresponding to the arachnoid membrane with scanty sub-dural and sub-arachnoid spaces. The pial sheath sends supporting septa into the interior of the nerve, and at about 15 or 20 mm. from the eyeball a large process of the pial sheath passing obliquely forwards carries the central retinal artery and vein into the middle of the nerve, and thence onwards along the axis of the nerve to the retina.

The nerve fibres, for the most part of very small diameter, $2\,\mu$, though a few are larger, $5\,\mu$ or $10\,\mu$, are up to the eyeball medullated fibres, but as in the brain and spinal cord possess no neurilemma. They are supported by neuroglia very similar to that of the spinal cord, and continuous with the pial septa, which like those of the spinal cord are irregular, the arrangement, so common in an ordinary nerve, of definite longitudinal bundles, each with its own sheath, being absent.

The number of fibres in the whole nerve has been calculated to be about 500,000; but higher estimates have been made.

Where the nerve joins the eyeball the dural sheath becomes continuous with the sclerotic coat and the pial sheath with the choroid coat, fine bundles from the sclerotic and also to some extent from the choroid passing transversely into the nerve and forming a network, the "lamina cribrosa." At this level the fibres of the nerve suddenly lose their medulla and pass on to the retina as naked axis cylinders supported by neuroglia; owing to the loss of medulla the thickness of the nerve is greatly diminished.

The medullaless fibres pass on to the level of the anterior, inner surface of the retina, forming the *optic disc* or optic papilla, in the centre of which lie the central artery and vein. From the optic disc the fibres radiate in curves, giving a pattern not unlike that known as 'engine-turned,' over the retina as far as the ora serrata, and form on the anterior, inner side of the retina, next to the vitreous humour, a layer which we shall describe presently as 'the layer of optic fibres.' Thus the optic nerve spreads itself out as a thin film lining the interior of the retinal cup next to the vitreous humour; and the other structures of the retina, in which the fibres end, lie outside or behind this film, between it and the choroid.

§ 738. *The Layers of the Retina.* Vertical sections of the retina, which has an average thickness of about ·15 mm., shew that it is made up of a series of layers superimposed, the one on the other; and the broad features of the layers are very much the same over the whole extent of the retina except at one part, the *macula lutea*, containing the depression called the *fovea centralis*. The structure of this part differs materially from the rest of the retina, and we must consider it by itself; but we may treat of all the rest of the retina surrounding the optic disc as one.

*The layer of optic fibres* (Fig. 154, I.) lies, as we have said, next to the vitreous humour and forms what we may henceforward call the innermost layer. Next to this comes a layer in which relatively large branched nerve cells are present; this is the *layer of ganglionic corpuscles* (Fig. 154, II.). It is succeeded by a peculiar layer, very closely resembling the molecular layer of the cerebellum (§ 648) and the ground-substance of the cortex (§ 649), and hence called the *molecular layer* or *reticular layer* (Fig. 154, III.), or to distinguish it from another somewhat similar layer, the *inner molecular layer* or *inner reticular layer*. Next comes a layer characterised by the presence of conspicuous nuclei closely packed together (Fig. 154, IV.), and still farther outwards lies a similar but somewhat different second layer (Fig. 154, VI.) of closely packed nuclei. The first is called the *inner nuclear layer*, or sometimes the "inner granular layer," the second the *outer nuclear layer*, or sometimes "the outer granular layer." The two layers in question are separated from each other by a layer (Fig. 154, V.) often very thin, which since in some of its features it resembles the inner molecular layer, is called the *outer molecular layer*, or "outer reticular layer;" it is sometimes called the "fenestrated layer or membrane." Outside the outer nuclear layer comes the remarkable *layer of rods and cones* (Fig. 154, VII.) which is the last of the layers of the retina proper; this is in turn succeeded by the *layer of pigment epithelium*, beyond which we come at once upon the limiting membrane of the choroid, the so-called membrane of Bruch (§ 713).

As we shall see, there is a functional connection, even if not actual continuity of structure, between the optic fibres on the inside and the rods and cones on the outside. As we shall see, the processes through which the rays of light are able to give rise to visual impulses begin in the region of the rods and cones; the rays of light have to pass through the whole or nearly the whole of the thickness of the retina before they begin their work; their work begun in the rods and cones is carried back through the thickness of the retina to the optic fibres and gathered up from the layer of optic fibres to the optic disc and so to the optic nerve. It is a necessity therefore that all the several elements of the retina should be very transparent.

We have already called the retina a piece of the brain; and even the brief statement which we have just made helps, from the likeness to cerebral structures which it suggests, to justify such a view. It is not surprising to find that in the retina as in the brain purely nervous elements are mixed with neuroglial elements, and that further, as in the brain, great difficulty is often met with in determining exactly which structure is really nervous and functional, and which merely neuroglial and sustentative. The broad distinctions however are easy.

§ **739**. *Supporting* or *Neuroglial Elements.* We apply the term neuroglial to all those elements of the retina which, though not nervous in nature, are derived from epithelial cells and not of mesoblastic origin. The inner surface of the retina, that which lies in contact with the hyaloid membrane investing the vitreous humour, is defined by a thin transparent membrane of a cuticular nature, the *inner limiting membrane* (Fig. 154, *m.l.i.*). Between the outer nuclear layer and the layer of rods and cones lies a somewhat similar thin transparent membrane, the *outer limiting membrane* (*m.l.e.*), pierced with holes for the passage of the inner parts of the bodies of the rods and cones, the greater part of the bodies of which lie outside the membrane plunged, as we shall see, in the pigment epithelium. These two membranes correspond to the inner and outer surface of the inner (anterior) wall of the retinal cup, which we have said (§ 703) alone furnishes the retina proper. The rods and cones therefore may be said to project beyond the retina, and indeed, when the development of the retina is traced out, we find that the rods and cones do really grow out from the inner wall of the retinal cup and thrust themselves into the outer wall, which is wholly transformed into the pigment epithelium.

Stretching radially from the inner to the outer limiting membrane in all regions of the retina, and therefore seen in a vertical section as vertically disposed structures, are certain peculiar shaped bodies known as the *radial fibres of Müller* (Fig. 154). Each fibre is the outcome of the changes undergone by what was at first a simple columnar epithelial cell. The changes are in the main that the columnar form is elongated into that of a more or less prismatic fibre, the edges of which become variously branched, and that while the nucleus is retained the cell-substance becomes converted into neurokeratin (see § 563). And indeed at the ora serrata the fibres of Müller may be seen suddenly to lose their peculiar features and to pass into the ordinary columnar cells which form (§ 714) the pars ciliaris retinæ.

At the inner limiting membrane, the fibre of Müller begins with a broad expanded foot fused with the membrane; indeed the inner limiting membrane may be regarded as in reality formed out of the coalesced broad more or less polygonal bases of the fibres of Müller. From this broad base the fibre narrows to a thin columnar body stretching radially outwards through the layer of optic fibres and that of ganglionic cells. From the edges of the body numerous fine processes extend in various directions, affording support to the optic fibres which wind in and out between the feet of, and to the ganglionic cells which are lodged in the spaces between the bodies of these fibres of Müller. Stretching still radially outwards the fibre as it passes through the inner molecular layer gives off processes which either divide into or at least are lost in the numerous neuroglial fibres forming part of the fibrillar structure of that layer. In the inner nuclear layer broader lateral processes become especially abundant, forming a neurokeratinal basketwork in the spaces of which the nervous elements of this layer are lodged; and here the body of the fibre bears the nucleus (Fig. 154 *n*) of the fibre itself, a somewhat elongated oval nucleus placed vertically. At the level of the outer molecular layer the body of the fibre breaks up into a thick spongework of delicate neurokeratin threads, supporting the nervous structures of the outer nuclear layer. At the outer limit of the nuclear layer this spongework seems to form the outer limiting membrane in the same way that the feet of the fibres form the inner membrane, while from the limiting membrane other processes, continuous with the spongework, pass up for a short distance to lie between the inner limits of the rods and cones.

Each fibre of Müller may be regarded as a brace or tie between the inner and the outer limiting membrane, its nucleus appearing among the nuclei of the inner nuclear layer, and its numerous processes on the one hand contributing to form the inner and outer molecular layer and on the other hand affording throughout the thickness of the retina a support for the nervous elements.

Besides these conspicuous fibres of Müller, which we may regard as large neuroglial elements, small, more ordinary neuroglial cells are also present in the various layers, especially perhaps in the outer molecular layer and in the layers of optic fibres and ganglionic cells. In addition to these neuroglial elements the retinal blood vessels as we shall presently see carry with them a small amount of actual connective-tissue.

§ **740**. *The Nervous Elements.* As we have said, there is at least a functional continuity between the rods and cones on the outside and the optic fibres on the inside. The structures of the outer nuclear layer are on the one hand closely and obviously continuous with, indeed form part of, the rods and cones, and on the other hand are if not actually continuous at least functionally connected across or by means of the outer molecular layer with the structures of the inner nuclear layer; while these in turn make connections, across or by means of the inner molecular layer, with the optic fibres either indirectly through the nerve cells of the ganglionic layer or in a more direct manner.

*The rods and cones.* Each *rod* consists of at least two quite distinct parts, of wholly different natures, called respectively the outer and the inner limb. The *outer limb* (Fig. 154, *r.o.*) is a cylinder, in man about 30 $\mu$ in length by 2 $\mu$ in diameter, which when seen in a natural condition is transparent, though highly refractive, and also doubly refractive. In prepared specimens it often appears fluted or grooved lengthwise and is very apt to cleave transversely into discs or fragments of varying thickness. It is probably made up of a number of excessively thin discs, ·6 $\mu$ or less in thickness, superimposed on each other and united by some kind of cement substance. The material of which the limb, as a whole, is composed stains deeply with osmic acid, but not at all with carmine and similar staining reagents, and is of a peculiar nature, in many respects resembling but still differing from the medulla of a medullated nerve. It is sensitive to light, swelling up when in the living eye it is exposed to light and shrinking again when the light is removed. During life it is coloured with a pecular pink colouring matter of which we shall treat later on, called visual purple, and which as we shall see is bleached by the action of light.

The *inner limb* (Fig. 154, *r.i.*) is an elongated ellipsoidal or fusiform body, about as long as, and at its broadest part slightly broader than, the outer limb, being truncated at its outer end, where by a flat surface it lies in contact with the inner end of the outer limb. It is of a wholly different nature from the outer limb, staining with carmine and other staining reagents, and having the ordinary optical features of protoplasmic cell-substance. The outer part lying next to the outer limb exhibits a longitudinal striation or fibrillation, but the inner part is faintly and finely granular, the whole however being very transparent. This slight difference of marking indicates a division of the inner limb into an outer and an inner moiety differing in nature from each other; and in some animals the outer part is occupied by a distinctly differentiated structure, called the "ellipsoidal body."

The inner end of the inner limb, piercing the external limiting membrane, narrows rapidly to a delicate thread *r.f.*, which is directed straight inwards towards the outer molecular layer, is

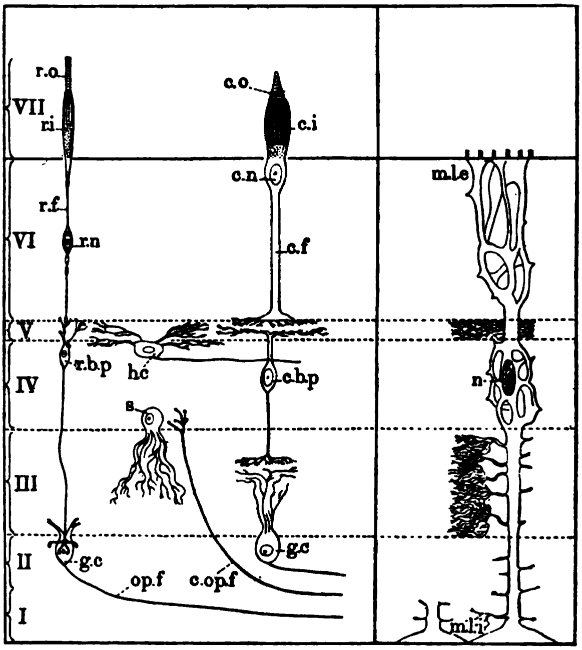

Fig. 154. Diagram to illustrate the Structure of the Retina.

The figure is quite diagrammatic and is introduced simply to assist in the description of the probable structure of the retina.

The several "layers" are indicated by the numeral I, &c. in order from within (vitreous humour) outwards.

On the right-hand side is shewn a fibre of Müller reaching from the inner limiting membrane *m.l.i.*, formed by the coalescence of its feet, to the outer limiting membrane *m.l.e.*; the lateral processes of the fibre are indicated, as well as the neuroglial fibrils (possibly independent of the fibres of Müller), in III. the inner molecular, and V. the outer molecular layer. *n.* the nucleus of the fibre of Müller.

On the left-hand side the nervous elements are represented. A rod with its *r.o.* outer, and *r.i.* inner limb, continued on as the rod fibre *r.f.* with its banded nucleus *r.n.*; also a cone with its outer *c.o.* and inner *c.i.* limb, and cone fibre *c.f.* with the nucleus *c.n.*

In IV., the inner nuclear layer, are represented, (1) the two kinds of bipolar cell, one connected with the rod fibre, *r.b.p.*, and the other with the cone fibre, *c.b.p.*; (2) a cell, *h.c.*, with horizontal dendrites running up into V., the outer molecular layer, and with a horizontal axon, running to the right; (3) a spongioblast with dendrites passing inwards into III., the inner molecular layer; and (4) the termination of a centrifugal optic fibre *c.op.f.*

In II., are shewn two ganglionic cells, *g.c.* with axons becoming optic fibres *op.f.* One ganglion cell shews the termination of the rod-bipolar cell close to its body, the dendrites of the other pass upwards to form a synapsis in the inner molecular layer with the termination of the cone-bipolar cell.

often varicose, and has otherwise much the appearance of a fine nervous filament. It ends at the inner limit of the external nuclear layer in a round or oval knob. This process of the inner limb, known as the *rod fibre*, bears at some part of its course, sometimes nearer the external limiting membrane, sometimes nearer the outer molecular layer, an oval nucleus *r.n.* over which the fibre expands to form a very thin layer of cell-substance. The nucleus is peculiar inasmuch as its staining, chromatin, constituents are, at least frequently, arranged in transverse bands, giving the stained nucleus a banded appearance, like that of the planet Jupiter.

Obviously we may consider the 'rod,' taken as a whole, to be an elaborated epithelium cell, whose nucleus lies on its inner thread-like continuation or rod fibre on the inner side of the external limiting membrane and contributes to the nuclei of the outer nuclear layer, and whose main body, lying outside the external limiting membrane, is sharply divided into an inner part, inner limb, which remains more or less protoplasmic in nature, and into an outer part, outer limb, which has undergone a differentiation having a certain resemblance to cuticular differentiation but still of a distinctly peculiar kind. Between the outer and inner limb there appears to be a distinct break; the two are in apposition but are not continuous; and indeed in some creatures, such as birds, the two are not even in apposition, being separated from each other by the intercalation of a spherical globule of a fatty nature often coloured. The most characteristic feature of the outer limb is the presence of visual purple, the importance of which will be indicated later.

A cone, like a rod, consists of an outer and an inner limb. The outer limb (Fig. 154, *c.o.*) is conical, not cylindrical in form, and, though much shorter than the outer limb of the rod, being in man about 10 $\mu$ in length, is in nature in every way similar to it save that it contains no visual purple. The inner limb *c.i.* is almost in all ways like the inner limb of a rod, save that it is usually broader, the diameter of the cones (outside the fovea) being about 6 $\mu$. Piercing the external limiting membrane it narrows to a fibre, *cone fibre*, *c.f.*, which however is broader than a rod fibre, and the oval nucleus *c.n.* which it bears, usually close under the external limiting membrane, is not banded and contains a conspicuous nucleolus. On reaching the outer molecular layer the cone fibre expands into a sort of foot, which gives off a number of fibrils running chiefly in a horizontal direction.

Over the retina (we are now, it will be remembered, excluding the macula lutea) the rods are much more numerous than the cones, there being about two or three rods in the line joining two cones, and since the outer limbs of the cones are much shorter than those of the rods, a surface view of the retina seen from the outside shews nothing but rods when the tops of the rods are in focus; if the focus be carried lower down, inwards, the cones will come into view and a mosaic of rods with cones interspersed between them will be seen. Towards the extreme periphery of the retina the cones become relatively more numerous, and close to the ora serrata are alone present. The total number of cones has been calculated to be more than three million.

To complete the account of the layer of rods and cones, we may add that the outer limbs and also, to a certain extent and under certain conditions, of which we shall speak later on, the inner limbs are imbedded in the layer of pigment epithelium, and that between the inner limbs a number of fine acicular cilia-like processes, apparently of cuticular nature, start up from the external limiting membrane, forming a sort of basketwork support for those structures; on the other side of the limiting membrane, as we have already said, all the nervous structures of the outer nuclear layer, that is to say the rod fibres and cone fibres with their respective nuclei, are supported by a sponge-work of neurokeratin proceeding from the fibres of Müller.

§ **741.** The nuclei of the *inner nuclear layer*, with the exception of the nuclei of the fibres of Müller, which, as we have said, are placed in this layer, belong to cells in which the amount of cell-substance is in most cases small compared to the nucleus. These cells are arranged in several tiers and, though possessing a general resemblance to each other, are not all of the same kind.

In the cells (Fig. 154, *c. b. p.* and *r. b. p.*) which form the greater number of the tiers, all in fact except the innermost and outermost tiers, the nucleus, round and highly refractive, is surrounded by a thin layer of cell-substance, which is prolonged in a radial direction from the opposite poles of the nucleus into an outer or peripheral and an inner or central process. From their possessing two obvious processes running in two opposite directions these cells have been called the *bipolar* cells of this layer.

These bipolar cells are of two kinds, one especially connected with the cones and the other with the rods, and they may be spoken of as cone-bipolars and rod-bipolars respectively. The peripheral process of the cone-bipolar is directed straight towards the outer molecular layer close to which it divides into a number of processes which spread out in a horizontal direction underneath the foot of a cone fibre. These processes intertwine with those of other bipolar cells in the outer molecular layer and the processes of one bipolar cell come into relation with the ends of several cone fibres. The central process, thinner and more delicate than the peripheral one and frequently varicose, is directed straight inwards to the inner molecular layer, and after traversing that layer for some distance without dividing, ends in very varicose branches which come into relation with the peripheral processes of the cells of the ganglion layer. We may consider the peripheral process as a dendrite, with which the cone fibre, or axon of the cone-cell forms a synapsis and similarly the central process as an axon forming a synapsis with the dendrites of a ganglionic cell. It has been found that the synapses formed in this way are seated at different depths in the inner molecular layer, some of the central processes of the bipolars penetrating this layer more deeply than the others.

The peripheral process (or dendrite) of the rod-bipolar divides soon after leaving the body of the cell into branches which ascend almost vertically through the outer molecular layer. These branches divide and subdivide till they finally terminate in fine delicate processes which surround the knobbed endings of the rod fibres. The processes of the smaller bipolar cells form in this way synapses with three or four rod fibres while the largest cells may come into relation with as many as 15 or 20. The central process (or axon) passes downward through the whole length of the inner molecular layer and terminates near the ganglion cell in thick branches with round or oval endings.

A third variety of very large bipolar cells, apparently connected with the cone fibres, has also been described.

In the outer part of the inner nuclear layer are cells differing from each other in several respects, but all agreeing in the general feature that their processes run mainly in a horizontal direction; these cells may therefore be spoken of as horizontal cells. Their bodies (Fig. 154, *h.c.*) are somewhat flattened in the plane of the retina, and those of the outermost tier encroach on the outer molecular layer. They give off on each side branching dendritic processes which pass in a more or less horizontal direction into the outer molecular layer and help to form the tangle of which that layer consists. Some of these cells also give off, usually from one side, an axon, which in most cases can be seen to run in a horizontal direction for some distance and then to terminate in fine branches; but we do not know definitely whether these axons come into relation with any special cells of this layer. The axons of other horizontal cells pass obliquely towards the centre of the inner nuclear layer before becoming horizontal, but there is no evidence that the axons of any of these cells pass in a central direction out of this layer.

The cells of the innermost tier of the inner nuclear layer (Fig. 154, *s.*) have nuclei which are round and refractive with conspicuous nucleoli and vary considerably in size. They are characterised by the absence of an axon, and have consequently been termed amacrine[1] cells. They have also been called "spongioblasts," and have been supposed to be concerned in the maintenance of the neuroglial framework; but they are probably nervous in nature. They give off dendritic processes which pass into the inner molecular layer, terminating at different depths either in fine processes which often run horizontally for

[1] from *α*, *μακρός*, and *ἴς*, a fibre.

considerable distances or in short branches with knobbed endings. The longer branches traverse the whole thickness of the molecular layer.

Thus while the nuclei of the outer nuclear layer are nuclei of the rod fibres and cone fibres, the nuclei of the inner nuclear layer are the nuclei of cells of a peculiar character; most of them belong to cells called bipolar, some of them, the innermost, belong to so-called 'amacrine' cells, while the outermost belong to a third kind of cell characterised by processes running in a horizontal direction. In several respects this inner nuclear layer resembles the nuclear layer of the superficial grey matter of the cerebellum.

§ **742.** The *layer of ganglionic cells* is closely connected with that of the *optic fibres.* The latter (Fig. 154, *op. f.*) consists, as we have said, of nerve-fibres, that is of naked, varicose axis cylinders without medulla and without neurilemma, radiating in all directions from the optic disc. Over the retina generally these fibres exist as a single layer of bundles, arranged in a plexiform manner, winding between the feet of the fibres of Müller, and supported by a neuroglia to which the processes of the fibres of Müller contribute, as well as by a scanty amount of connective-tissue belonging to the retinal blood vessels. The fibres and bundles of fibres become less numerous, and the plexuses more open, from the optic disc towards the ora serrata, and at the latter line cease altogether. The diminution is due to the optic fibres continually passing away from the layer into the other, outer layers.

The *layer of ganglionic cells* is over the retina generally a single layer of nerve cells. Each cell (Fig. 154, *gc.*), 30 $\mu$ or so in diameter, consists of a cell-body which is transparent or nearly transparent, though sometimes containing pigment, and a relatively large spherical nucleus. The cell-body sends inwards a single undivided axon which becomes an optic fibre, and outwards a number of dendrites, which, passing into the inner molecular layer and dividing, in different zones of the layer, into delicate filaments, form synapses with the bipolar cells as already described. The dendrites of one ganglion cell spread out over a considerable area in the molecular layer and this makes it probable that each ganglion cell forms synapses with several bipolar cells. It is probable that one ganglion cell forms synapses in this way with several rod-bipolar cells and another with several cone-bipolar cells, but it has also been stated that one ganglion cell may form synapses with bipolar cells of both rods and cones. These ganglionic cells are far less numerous than the optic fibres, so that only some of the latter are continued into the former; some of the optic fibres (Fig. 154, *c. op. f.*) pass directly from the nerve fibre layer into the inner molecular layer and after traversing this layer, terminate in free knobbed endings at the inner limit of the inner nuclear layer. It has been stated that they form synapses with the amacrine cells of this layer, while on the other hand it is said that in the bird they form synapses with the horizontally disposed dendrites of special cells. These fibres are supposed to carry nervous impulses from the central nervous system to the retina, and may be spoken of as "centrifugal optic fibres." Other fibres have been described as passing directly into the molecular layer, within which they take a horizontal direction, but it is not known how such fibres terminate.

§ **743.** We may then consider the retina as made up of three main layers of cells; (1) the rods and cones with the outer nuclear layer, and (2) the cells forming the inner nuclear layer, and (3) the ganglionic cells with the optic fibres. On theoretical grounds we may conclude that these three layers are functionally continuous, that changes set going in the rods and cones sweep through the inner nuclear layer, and issue along the fibres of the optic nerve as nervous impulses, and it appears that the changes set up in the cones and rods respectively travel along different paths. In each of these paths there are two breaks in the two molecular layers, one where the cone or rod fibres form synapses with the bipolar cells and one where the bipolar cells form synapses with the ganglionic cells. These two molecular layers repeat, in the outlying part of the brain which we call the retina, some of the characteristic features of the brain itself. Each layer may, like the molecular layers of the cerebrum and cerebellum, be regarded as a mass of synapses imbedded in neuroglia, but as in the corresponding central structures we cannot distinguish neuroglial from nervous elements.

We have reason to think that the molecular changes which light induces in the rods and cones differ very considerably in character from the molecular changes in the fibres of the optic nerve which constitute a nervous impulse, and that the transformation from the one set of changes to the other is effected through some or other of the retinal structures which we have described. But we cannot attribute definite functions to the several elements; but one fact may be pointed out which shews how complex are the relations of these elements. It seems probable that each ganglionic cell forms synapses with several cone-bipolar cells or with several rod-bipolar cells, or even with the bipolars of both cones and rods. Again, there is little doubt that each cone-bipolar cell forms synapses with several cone fibres, and that one rod-bipolar may communicate with many rod fibres, so that each ganglionic cell is in direct functional continuity with many cones or rods or with both cones and rods. The cells with horizontal processes lying in the outer part of the inner nuclear layer probably form another means by which different cells of the retina (possibly cones and rods) are brought into relation with one another. Of the nature of the changes taking place in this complicated structure we know nothing; it can only be suggested that the primary changes set up by light in the rods and cones undergo repeated differentiation and elaboration in passing from unit to unit.

§ **744.** *The Macula Lutea and Fovea Centralis.* On the temporal side of the optic disc, at a distance of about 4 mm. from, and a little below the horizontal level of, its centre an oval area, with its long axis of about 2 mm. placed horizontally, is distinguished from the rest of the retina by its yellowish or brownish tint; this is the *macula lutea* or 'yellow spot.' At the edges of the macula the retina is thickened but in the centre becomes very thin. So that the macula presents a central depression, about ·3 mm. in diameter, the *fovea centralis*, surrounded by a raised rim.

A vertical section through the macula lutea shews that, in contrast to the retina generally, in which the rods are more numerous than the cones, in the very centre of the fovea cones alone are present; their outer limbs, however, are very elongated, 60 $\mu$ long by 2 $\mu$ or 3 $\mu$ broad, and indeed are rod-like. Moreover, all the several layers of the retina described above are here absent except the layer of cones. and the outer nuclear layer or layer of cone fibres. Between the pigment epithelium and the vitreous humour are found only these elongated cones, with the nucleated cone fibres belonging to them; the latter supported by a delicate reticular neuroglia curve away towards the periphery of the fovea; next to the vitreous humour lies an exceedingly thin layer of neuroglia. About 7000 cones are supposed to be crowded together in the very centre of the fovea.

A vertical section through the thickened rim of the macula shews all the layers present, the layer of ganglionic cells being exceedingly prominent and consisting not as elsewhere of a single layer or at most of two layers but of several, eight or nine, layers of cells; indeed the greater thickness of the retina at the rim of the macula is chiefly due to an increase in the layer of ganglionic cells, the inner nuclear layer being somewhat increased, but not to any great extent, and the others hardly at all. In the layer of rods and cones, the cones are more numerous than outside the macula, and their outer limbs are somewhat elongated; but otherwise the features of the several layers are the same as in the retina generally; we may add, however, that the ganglionic cells appear bipolar rather than multipolar, one process being continued as elsewhere into an optic fibre and the other directed obliquely towards the central parts of the macula; the latter process, however, sooner or later divides into fine branches.

If in a vertical section taken across the whole macula we examine the features of the section from the periphery towards the centre, we find the layer of optic fibres rapidly thinning out and soon disappearing, and the layer of ganglionic cells, after its temporary thickening, also thinning out and disappearing. The inner molecular layer and the inner nuclear layer extend a little farther towards the centre, but these also eventually disappear, all that is left of them and of the outer molecular layer being the thin layer of neuroglia mentioned above. At the same time the rods, relatively numerous at the peripheral parts of the macula, gradually grow scanty and finally disappear. In this way nothing is left in the fovea itself but the cones and the cone fibres.

Over the retina generally the several elements seem, as seen in a vertical section, to be disposed vertically the one over the other. During the thinning out and disappearance just mentioned, this vertical disposition of the several elements gives way, except so far as the cones themselves are concerned, to an oblique disposition, which becomes the more marked as the centre is approached. It is as if the parts of the inner nuclear layer, of the inner molecular layer and of the ganglionic layer belonging to the cones and cone fibres of the central region of the macula were dragged on one side towards the periphery. We may imagine that each (rod or) cone with its (rod or) cone fibre is connected in some way or other with one or more of the cells of the inner nuclear layer, and so with one of the ganglionic cells; over the retina generally these are placed in the same vertical line, and before a ray of light can act on the rod or cone it must pass through these several other structures. In the fovea these other structures are pulled on one side, so that in the very centre of the fovea the light can gain access to the outer limb of the cone, without having to pass through any other structures than the cone itself and its cone fibre. This oblique disposition is also obvious in the cone fibres, which elsewhere short and vertical are in the fovea much elongated, and radiate obliquely from the centre of the fovea to their more peripherally placed inner nuclei or other structures with which they have to make connections of some kind or another.

The colour of the macula which is said to be in the living eye brown rather than yellow is most intense in the thickened rim, fading gradually away peripherally and centrally. It is said to be wholly absent from the central fovea, but this is doubtful. The colour is due to a pigment diffused through the layers lying to the inside of the outer nuclear layer, being absent from this layer as well as from the cones themselves; hence the diminution of the colour in the very centre. The pigment seems to be attached at least as much to the neuroglial as to the nervous elements. It thus presents a contrast to the visual purple which is limited to the outer limbs of the rods, not being present elsewhere, not even in the outer limbs of the cones.

§ **745.** *The Blood Vessels of the Retina.* The central artery and vein of the retina running, as we have seen, with their sheath of connective-tissue in the middle of the optic nerve reach the surface at the centre of the optic disc, which is excavated so that the blood vessels seem, on a surface view of the retina, to arise out of a minute crater. Both artery and vein divide into two main trunks, one directed upwards and the other downwards, the division of the vein taking place while it is still imbedded in the nerve; each trunk divides again into two, and these into several branches which are distributed over the retina as far as the ora serrata, the branches on the nasal side radiating in a more or less straight direction, while those on the temporal side arch round above and below the macula lutea, veins and arteries taking much the same course.

Both arteries and veins run close to the internal limiting membrane in the layer of optic fibres, being accompanied by sheaths of delicate connective-tissue enclosing perivascular lymphatic spaces. The capillaries into which the arteries break up, and from which the veins are gathered up, form in the first instance a somewhat close capillary network between and among the optic fibres and ganglionic cells; but the vessels also extend a certain distance outward and form a second outer, also fairly close capillary network in the inner nuclear layer. Some of the loops may reach the outer molecular layer, and in some few animals capillaries may be seen in the outer nuclear layer. In no case do they extend beyond the external limiting membrane, and as a rule the outer molecular layer may be taken as marking the limit beyond which they do not extend.

The arteries and veins sweep, as we have said, round the macula lutea, which however is largely supplied by two small arteries and veins coming straight from the optic disc. Capillaries extend into the margin of the macula, reaching as far as the layers of ganglionic cells and the inner nuclear layer; from the fovea itself, blood vessels are wholly absent.

§ **746**. *The Pigment Epithelium.* This is a single layer of epithelium cells lying between the rods and cones of the retina proper on the inside and the limiting membrane of the choroid, membrane of Bruch, on the outside. It is wanting where the optic nerve passes forward to join the retina, but is present, and exhibits the same features over the whole of the retina up to the ora serrata, at which line it passes into the more ordinary pigment epithelium of the ciliary processes.

It very readily separates from the choroid, and frequently comes away with the retina when the latter is removed from the eyeball. In such cases the layer is, in a surface view, seen to be composed of cells which have a polygonal outline and are loaded with black pigment granules, the nucleus of the cell being more or less obscured by the pigment, and the outlines of the cells being well defined by clear lines of cement material, apparently neurokeratinal in nature, free from pigment; a similar appearance is presented by the pigment epithelium of the ciliary processes, though the outlines are not so well marked.

A vertical section however taken through the layer in position shews that the cells possess peculiar features absent from the simpler epithelium beyond the ora serrata. Each cell is seen to consist of a more or less cubical body, the outer part of which next to the choroid is free from black pigment, though often containing small irregular masses of yellowish material of a fatty nature allied to the medulla of nerves. The inner part, that next to the retina, is on the other hand loaded with black pigment granules, which on closer examination are found to be minute crystals; the substance of which these are composed is called *fuscin*. The nucleus lies either wholly in the clear part or partially imbedded in the pigment.

The most important feature of the cell however is that the inner surface next to the retina is not smooth and even, but frayed out into a number of rod-like or filamentous processes, each carrying a load of pigment crystals. Further, when eyes are subjected immediately before death to different conditions as regards light, these processes are found in different states.

If an eye be fully exposed to light before removal and examination, the processes carrying pigment are found to stretch a long way inwards between the outer limbs of the rods and cones, investing these outer limbs with a sheath of pigment, and even reaching between the inner limbs. If, on the contrary, the eye be kept in the dark before removal and examination, the processes are found to be short and to stretch a little way only inwards, not reaching much farther than the tops of the outer limbs of the rods and cones. The substance of the cell has in fact the power of amœboid movement, at one time throwing out long filamentous processes inwards between the rods and cones, and at another time retracting the processes into the body of the cell. As they move to and fro these processes carry with them the crystals of pigment with which they are studded; hence in the extended condition much of the pigment is carried away from the body of the cell inwards between the rods and cones, leaving the nucleus less covered with pigment, while in the retracted condition the pigment is carried back to the body of the cell and the nucleus becomes obscured. Further, while various circumstances may determine whether the processes are extended or retracted, the falling of light on the retina has the most marked and potent effect. When light falls on the retina the processes hurry inwards and envelope the outer limbs of the rods and cones with pigment; when the light is shut off from the retina the processes carry back the pigment to the body of the cell.

Hence in an eye exposed to light the processes and pigment being largely jammed in between the outer limbs of the rods, and these outer limbs at the same time swelling, the pigment epithelium adheres closely to the retina, and when the retina is removed is carried away with it. In an eye kept in the dark, the processes being withdrawn, and the outer limbs of the rods shrinking again, the attachment of the retina to the epithelium is much less, and the retina can be more readily removed, so as to leave the pigment epithelium adherent to the choroid.

We may add that this shifting of the pigment may be seen to be accompanied by a change of form in the inner limbs of the cones. Under the influence of light the inner limb becomes shorter and broader, in fact contracts, and when the influence of the light is removed elongates to its original length. Moreover these changes in the cones may be induced, not only by light falling on the retina, but also, through a mechanism not at present fully understood, as the result of stimulation of the skin, by light or otherwise; in these latter cases the change of form of the cone is not necessarily accompanied by migration of the pigment. These changes in the cones and pigment have also been found to take place in both eyes when only one eye is stimulated by light and it is probable that the change produced in the unstimulated eye, both in this way and by stimulation of the skin may be brought about by impulses travelling along the centrifugal optic fibres (§ 742).

## SEC. 7. ON SOME GENERAL FEATURES OF VISUAL SENSATIONS.

§ **747**. When light falls upon the retina it produces, under favourable circumstances, a change in our consciousness which we call a sensation of light, a visual sensation. The immediate effect of the light is to stir up certain changes in the retina; these retinal changes give rise in turn to nervous changes in the optic fibres; these latter, which we have called 'visual impulses,' start in the brain a further series of events, one effect of which is a change in our consciousness; and it is this change in our consciousness which we call a sensation. We may, and often do, speak of light as a 'stimulus' to the retina, the result of the stimulation being visual impulses; but we may also speak of light as a stimulus to the whole visual apparatus, central as well as retinal, regarding the sensation as if it were the direct and immediate, instead of being the indirect and ultimate effect of the stimulus. We may, by observing certain general features of visual sensations, such as can be ascertained by means of a direct and simple appeal to our own consciousness, study the relations which obtain between the characters of the stimulus on the one hand and those of the sensation on the other. There are certain advantages indeed in doing this before we proceed to discuss the nature of the changes in the retina through which rays of light give rise to visual impulses in the optic fibres. But in taking this course we must bear in mind how complex is the whole process through which the stimulus gives rise to the sensation. We must remember that, as we have already said, though some of the characters of a visual sensation are impressed upon it while it is as yet immature, as yet in the stage of visual impulses, others are introduced later on in the course of the cerebral changes. Since we are now dealing for the first time with sensory impulses studied in this way, we may venture to enter into some details, for the deductions which may be drawn concerning visual sensations will apply to a large extent to other sensations.

To simplify matters we will in the first instance suppose that the luminous object, the object emitting or reflecting light, is so small that the image of it on the retina may be considered as a mere point; we may speak of it as a luminous point. If for the sake of illustration or otherwise we have to consider a larger luminous object, we shall do so without regard to the size of the image on the retina unless this is specially mentioned.

We may begin with the preliminary remark that in dealing with light as a stimulus of visual sensations, we have to consider not only the intensity of the stimulus but also its duration. A luminous point may appear dim and feeble, that is to say, the waves of light from it have a small amplitude and so bring little energy to bear on the retina, or it may appear bright and strong, that is to say, the waves of light have a large amplitude and so bring much energy to bear on the retina. Whether dim or bright, the luminous point may act on the retina for a longer or a shorter time; and moreover, during its action may remain steady, not varying in intensity, or may vary in intensity and become unsteady or flickering. In estimating the total visual effect of a luminous point, we have to consider both these features, its intensity or brightness and its duration.

Neglecting for the present the feature of duration, we find that a luminous point must possess a certain amount of brightness in order to produce any conscious sensation at all, in order to be visible. If the waves of light fall on the retina with less than a certain amplitude, if their energy sinks below a certain minimum, they fail to give rise to visual impulses, or at least to such as can affect consciousness; for we may suppose that visual impulses might be generated and yet be so feeble as not to produce in the cerebral centre changes sufficiently great to affect consciousness. It will be understood, of course, that the exact degree of brightness at which the luminous point becomes visible depends on the greater or less irritability, on the sensitiveness, of the retina. The same amount of luminous energy which, falling on one retina or on one part of a retina, produces a distinct sensation, may, falling on a less sensitive retina or on a less sensitive part of the same retina, produce no sensation whatever.

After staying in the dark for some time the sensitiveness of the retina is greatly increased, and the alteration of sensitiveness occurring in response to alteration of illumination is usually spoken of as adaptation. An eye from which light has been excluded for some time is said to be adapted to darkness or dark-adapted. The increase of sensitiveness is more rapid during the first few minutes of darkness, but the eye continues to become more sensitive for about two hours, though after twenty minutes the change is very slight.

From the minimum onwards the intensity of the sensation increases with the luminous intensity of the object; a wax candle appears brighter than a rushlight, and the sun brighter than any candle; we are dealing now with the intensity of the light quite apart from the size of the luminous object. The ratio, however, of the sensation to the stimulus is not a simple one. If the luminosity of an object be gradually increased from a very feeble stage to a very bright one, it will be found that, though the corresponding sensations likewise gradually increase, the increments of the sensations due to increments of the luminosity gradually diminish, and at last an increase of the luminosity produces no appreciable increase of sensation; a light, when it reaches a certain brightness, appears so bright that if it becomes brighter we do not recognize that it is brighter. Hence it is much easier to distinguish a slight difference of brightness between two feeble lights than the same difference between two bright lights; we can easily tell the difference between a rushlight and a wax candle; but two suns, or even two bright lamps, one of which compared with the other gave out just that additional amount of light, just that additional quantity of luminous energy, which a wax candle gives out in addition to that given out by a rushlight, would appear to us to have exactly the same brightness. In a darkened room an object placed before a candle will throw what we consider a deep shadow on a sheet of paper or any white surface. If, however, sunlight be allowed to fall on the paper at the same time from the opposite side, the shadow is no longer visible. The difference between the total light reflected from that part of the paper where the shadow was, and which is illuminated by the sun alone, and that reflected from the rest of the paper which is illuminated by the candle as well as by the sun, remains the same; yet we can no longer appreciate that difference because the whole surface has become so bright.

On the other hand, when we carefully compare the visual sensations excited by measurable differences of luminosity, we come upon the following remarkable result. If we place two candles so as to throw two shadows of some object on a white surface, the shadow caused by each light will be illuminated by the other light, and the rest of the surface will be illuminated by both lights. If now we move one candle away we shall reach a point at which the shadow caused by it ceases to be visible, that is to say, we fail at this point to appreciate the difference between the surface illuminated by the near light alone and that illuminated by the near light and the far light together. If now, having noted the distance to which the candle had to be moved, we repeat the same experiment with two bright lamps, moving one lamp away until the shadow it casts ceases to be visible, we shall find that the lamp has to be moved just as far as the candle; that is to say, the least difference between the illumination of the bright lamps which we can appreciate is the same as in the case of the dimmer candles. Many similar examples might be given shewing a similar result; in fact, it is found by careful observation that, within tolerably wide limits, the smallest difference of light which we can appreciate by visual sensations is a constant fraction (about $\frac{1}{100}$th) of the total luminosity employed. As we shall see, the same relation holds good with regard to the other senses as well. It may be put in a general form, as a law of sensation, often called Weber's law, somewhat as follows: The smallest change in the magnitude of a stimulus which we can appreciate through a change in our sensation always bears the same proportion to the whole magnitude of the stimulus. This law holds good within certain limits provided that time is allowed for the eye to become adapted to the change in illumination; it fails however when the stimulus is either above or below a certain range of intensity.

Hence, if we take the smallest difference which we can appreciate in a stimulus as a measure of our sensibility to differences in the stimulus, we may say that on the one hand in respect to absolute differences, such as that between two lamps and that between two rushlights, our sensibility varies inversely as the magnitude of the stimulus; we are more sensible of the same absolute difference when that is a difference between two rushlights than when it is a difference between two lamps. On the other hand, in regard to relative differences, our sensibility is independent of the magnitude of the stimulus; the difference of which we are sensible in the case of the lamp bears the same proportion to the whole luminosity of the lamp as the difference of which we are sensible in the case of the rushlight bears to the whole luminosity of the rushlight.

§ **748.** Returning now to consider the duration of the stimulus, as distinguished from its intensity, we find that a stimulus of extremely brief duration may give rise to a distinct sensation; the flash of an electric spark, for instance, is readily visible. There is probably a limit in respect to duration within which the stimulus fails to produce a sensation; it is probable, for instance, that a certain number of undulations in succession must fall on the retina in order to give rise to a visual sensation, and that a single undulation of the ether falling on the retina, if such a thing were possible, would produce no visual effect; but the exact limit will depend on the intensity and nature of the light, and we need not enter upon these details here.

It is of more importance to note that the visual sensation caused by a very brief stimulus lasts a considerable time; the sensation has a duration much greater than that of the stimulus. The sensation of a flash of light, for instance, lasts for a much longer time than that during which luminous vibrations are falling on the retina. In this respect, we may roughly compare a visual sensation to a simple muscular contraction caused by such a stimulus as a single induction shock. We might indeed construct a "visual sensation curve" very much after the fashion of a "muscle curve." We should find that after a very obvious latent period the sensation began, rose to a maximum, and then declined. This latent period forms an important part of the "reaction period," on which we dwelt in a former part of this work (§ 691). As we have said, in all the sensations with which we are now dealing, we have to distinguish at least two parts, the peripheral part, the events taking place in the retina, and the central part, the events taking place in the brain, the two being united by means of the visual impulses passing along the optic nerve. And within the latent period are comprised the changes in the retina which start the visual impulses, the passage of these impulses along the optic fibres, and the changes in the brain antecedent to consciousness beginning to be affected; of these the retinal changes probably take up the most time.

The length of the sensation, as compared with that of the stimulus, is illustrated by viewing objects in motion under a very brief illumination, such as that of a single electric spark. In such a case the light reflected from the object is sufficient to generate a distinct sensation, to give rise to a distinct image of the object, but it ceases before the object can make any appreciable change in its position, and the image accordingly is that of a motionless object. When a moving body is illuminated by several rapid flashes in succession, several distinct images corresponding to the positions of the body during the several flashes are generated; this, as we shall see presently, is because the images of the body corresponding to the several flashes fall on different parts of the retina.

The duration of the stimulus remaining the same, the characters of the sensation and the form of the sensation curve will, in accordance with what was stated above, vary with the intensity of the stimulus; a bright flash will produce a sensation greater and of longer duration than that produced by a feeble flash, the curve will be higher and more extended. We have reason to think, too, that the form of the curve is dependent on the intensity of the stimulus in such a way that the maximum is reached more quickly and the decline from the maximum begins earlier, and at all events in the first part of its course, is more rapid with the stronger than with the feebler stimulus.

When the stimulus is not a mere flash, but is of some duration leading to a prolonged sensation, we can readily distinguish between that part of the sensation which is going on while the light is still falling into the eye, and that part which goes on after the light has ceased to fall on the retina; this latter part is often spoken of as the *after-image.* When the light is very bright this "after-image" frequently becomes very prominent, even after a very brief exposure. Thus, if we look, even for a moment only, at the sun, and then immediately shut the eye, an intense visual sensation, a bright visual image of the sun, remains for some considerable time.

§ **749.** From the prolonged duration of visual sensations it results that when two or more stimuli, such as two or more flashes of light, follow each other at a sufficiently short interval, the two sensations or the several successive sensations are fused into one more or less uniform sensation. Thus a luminous point moving rapidly round in a circle gives rise to the sensation of a continuous circle of light. We might, in a very general manner, compare this with the way in which a series of simple muscular contractions resulting from rapidly repeated induction shocks are fused into a fairly uniform tetanus; this analogy, however, of the sensory with a muscle curve is open to objection and must not be taken too closely. When the stimuli succeed each other so rapidly that each sensation begins before its predecessor has had time to appreciably decline, the total sensation is as completely uniform as if the stimulus were constant. If the interval between each two stimuli be just so long that each sensation in turn has had time to distinctly diminish before the next sensation begins, the result is a "flickering;" and there are of course many degrees of flickering between a perfectly steady and an obviously intermittent light. The interval between successive stimuli at which fusion takes place and flicker disappears, varies according to the intensity of the light, being shorter with the stronger light; with a faint light it is about $\frac{1}{10}$ sec., with a strong light $\frac{1}{30}$ or $\frac{1}{50}$ sec., with very strong illumination the interval has to be made still shorter. This may be shewn by rotating rapidly before the eye a disc arranged with alternate black and white sectors of equal width. With a faint illumination, the flickering indicative of the successive sensations from the white sectors not being completely fused, ceases when the rotation becomes so rapid that each pair of black and white sectors takes only $\frac{1}{10}$ sec. in passing before the eye. When a brighter illumination is used the rapidity must be increased before the flickering disappears; this is owing to the decline of the stronger sensation, as stated above, beginning earlier and being more rapid than that of the weaker sensation.

Fusion not only takes place when white alternates with black, *i.e.* with alternating periods of illumination and absence of illumination, but also with alternating periods of more and less illumination. Thus when a stronger stimulus alternates with a weaker stimulus, a similar flickering will be seen at a certain rate of alternation, passing into a continuous sensation with increasing rapidity; and it is found that the point at which fusion of the stimuli takes place so as to give a continuous sensation varies with the difference of intensity between the two stimuli, the more nearly they approach one another in strength the more readily does fusion occur. As we shall see later (§ 756) colours fuse in a similar manner when they stimulate the retina alternately, and the point of fusion here shews a similar dependence on the difference of brightness of the stimuli.

**§ 750.** When a luminous point excites the retina, we recognize in the sensation not only the features of intensity, duration, and constancy or steadiness, but also a character which is dependent on the position in the retina of the image of the luminous point. We recognize the sensation caused by a luminous point whose image falls on the temporal side of the retina, as different and distinct from the sensation caused by a luminous point whose image falls on the nasal side of the retina, and so with other positions of the images; indeed, as we shall see presently, we are able to distinguish, to recognize as different and distinct, two sensations excited by two luminous points, the images of which lie very close indeed to each other on the retina. We distinguish the sensations, however, not by reference to the parts of the retina affected, but by reference to the relations in space of the luminous points giving rise to the sensations. Since this is a matter of some importance we may treat of it in some detail.

In the vast majority of cases the changes in the retina which give rise to visual impulses, and so to visual sensations, are brought about by light falling on the retina. But the retina may be stimulated by other agencies than that of light. When this is the case the changes in the retina, however produced, if they are able to affect consciousness at all, give rise to visual sensations, and to visual sensations only. A mechanical stimulation of the retina, as when a blow is struck on the eye, produces a visual sensation, a sensation of light; pressure exerted on the eyeball so as to produce pressure on the retina gives rise to visual sensations in the form of rings of light, of coloured light, known as 'phosphenes;' and when the retina is subjected in various ways to stress or strain, as by rapid accommodation, or by rapid movement of the eyeball from side to side, there often result visual sensations in the form of light of some kind or other, best appreciated when objective light is cut off from the retina and when the retina has by long repose been rendered unusually sensitive. Electrical stimulation also gives rise to visual sensations; not only is the induced current, or the break and make of a constant current, thus able to excite the retina, but during the whole time of the passage of a constant current of adequate strength, even though it remain of uniform intensity, visual impulses, and thus visual sensations, are being generated; in this respect the retina resembles sensory and differs from motor nerves. It is stated that when the current is directed from the layer of optic fibres to the layer of rods and cones, the sensation is a positive one, a sensation of light or of increased light, but that a current in the reverse direction gives rise to a sensation of diminished light, a sensation of darkness.

That the stimulation of retinal structures by other agents than light may thus give rise to visual sensations, and apparently to visual sensations alone, may be verified by experiment at any time. The occasions on the other hand are rare in which evidence can be gained as to whether stimulation of the optic nerve apart from the retina, whether stimulation of the optic fibres themselves, and not of their special endings in the retina, also gives rise to visual sensations and to visual sensations alone. In certain cases of removal of the eye it has been stated that when the optic nerve was divided in the absence of anesthetics, the patient "saw a great light" accompanied by no more pain than could be accounted for by the filaments of the fifth nerve which are distributed to the optic nerve as nervi nervorum. Such experiences are urged in support of the view that all impulses passing along the optic nerve however generated, whether by retinal changes or by other means, are visual impulses and visual impulses only; they give rise to visual sensations and to visual sensations alone. On the other hand, in other cases of removal of the eye in the absence of anesthetics, neither section of the optic nerve nor subsequent stimulation of the stump has given rise to visual sensations. We shall return to this question later on when we have to speak of what is known as the "specific energy of nerves," and have only referred to it incidentally now.

§ **751.** Visual sensations then may be produced in many other ways than by the falling of light on the retina; and the point to which we wish to call attention now is that we are unable to distinguish a sensation thus produced from the visual sensation produced by light itself. We cannot by the help of the mere sensation alone recognize the nature of the agency which has produced the changes in the retina giving rise to the sensation. The identity of sensations due to mechanical stimulation with those due to luminous stimulation may be illustrated by the story of the witness in a case of assault, who swore that he recognized his assailant by the help of the flash of light produced by a blow on his eye. Since light emitted or reflected from external objects is the normal stimulus for visual sensations, all our visual sensations seem to us to be produced by rays of light proceeding from external objects; we look for their cause not in the retina itself, but in the external world; and when we wish to know why we have felt the sensation of a flash of light, we ignore the retina and seek at once in the external world for some source of the rays of light corresponding to the sensation. Hence, also, when in a particular part of the retina, in a spot for instance on the nasal side of the right eye, changes take place such as would be produced by the image of a luminous point falling on that spot, though we recognize the sensation which results as having a certain feature, owing to its being started in that particular spot, we do not through the sensation learn anything about the retina itself, we do not through it recognize that the nasal side of the retina or any particular spot in the nasal side has been affected; what we do recognize, or infer, is the existence in the external world of such a luminous point as would give rise to the sensation in question. The dioptric arrangements of the eye are, as we have seen (§ 707), such that a luminous point in order to give rise to an image in the spot in question, and so to the sensation in question, must occupy a particular position on what we call the right-hand side of the external world. We accordingly recognize the sensation as having been caused by, or refer the sensation to, a luminous point having that position on our right hand. And so with the sensations similarly generated in all other spots in the retina; we recognize them as caused by luminous points occupying such positions in the external world that their images fall on those spots. In each case we ignore the retina itself, and the changes taking place in it are to us simple tokens of luminous events in the external world. When with the right eye we see a luminous point on our right-hand side, if we know that changes are taking place on the nasal side of the retina of that eye, it is not because we are directly aware that the nasal part of the retina is being affected, but because our knowledge of the dioptrics of the eye teaches us that the image of the luminous point is falling on the nasal side of the retina. If we are suffering from right-sided hemianopia (§ 670) all that our sensations can of themselves tell us is that we cannot see things on the right-hand side; they do not tell us anything about the retina itself; they cannot even tell us whether the deficiency of vision is due to changes failing to be set up in the retina or to the cerebral centres failing to be affected by the retinal changes; such questions we have to decide by some other means than a simple examination of our sensations, and by a similar roundabout way only are we able to conclude that in such a hemianopia it is the nasal side of the right retina, and the temporal side of the left retina, which fail to give rise to visual sensations. Our sensations, in fact, tell us of themselves nothing about the optical image on the retina; they do not tell us whether the retinal image is inverted or no; the fact that the retinal image is an inverted one does not in itself influence our visual sensations, and hence the inversion needs no correction on our part.

§ **752.** As we have just said, if the images of two luminous objects, two luminous points, fall on the retina at a certain distance apart, the consequent sensations are distinct. If, however, the two objects are made to approach each other, a point will be reached at which the two sensations are fused into one. Two stars at a certain distance apart may be seen distinctly as two stars, while two stars nearer each other appear to be one star; we cannot analyse the latter sensation into its constituent parts.

The angle which the line between two points must subtend in order that they may be distinguished, is known as the minimum visual angle, and this is the basis of visual acuity. Visual acuity may thus be tested by determining the distance at which two points cease to be distinguished; but the method commonly adopted is that of determining the distance at which certain objects, such as letters, cease to be recognized. This however is faulty, since the recognition of a letter is more a psychical than a physiological process. A better and equally convenient method is to determine the distance at which a black patch of a given size on a white ground (or a white patch on a black ground) can just be seen, *i.e.* distinguished from the ground.

Similarly, when the images of a number of luminous points, of equal luminosity, fall on the retina sufficiently near each other, the effect is not a number of sensations of luminous points, but one sensation, that of a luminous surface. This introduces a new feature of visual sensations, namely that of size. If the luminous points be few, so as to involve a small area of the retina, the sensation is that of a small surface; if the luminous points, equally near to each other as before, be numerous, so as to involve a large area of the retina, the sensation is that of a large surface. Moreover, such a sensation of a surface will be referred to some position in space corresponding, as we have just seen, to the region of the retina affected, and will possess features determined by the relative positions and so the figure formed by the luminous points; it will be the sensation of a surface of a certain form, round, square or the like; thus the retinal area stimulated supplies data, which are used, in a manner which we shall study later on, for judging the size and form as well as the position of visible objects.

When the images of two luminous points are at a certain distance apart on the retina, the two sensations may have no effect whatever on each other; but when they are within a certain distance from each other, the sensations do affect each other, in a manner which we shall study later on. Meanwhile we will merely say that when two images approach so closely that the two sensations become fused into one, such a mutual influence is exerted that the intensity of the total sensation produced is greater than that of either of the sensations caused by the single image, though less than the sum of the two A number of luminous points scattered over a wide surface would appear each to have a certain brightness; each would give rise to a sensation of a certain intensity. If they were all gathered into one spot, that spot would appear brighter than any of the previous points; the intensity of the sensation would be greater.

§ **753.** *The region of distinct vision.* The distance at which two images must be apart from each other in order that the two sensations may be separate is not the same for the whole area of the retina. If two luminous points lie near the optic axis, so that their images fall on the fovea centralis or on the yellow spot, they will be seen as two distinct points, even when their images lie very close indeed to each other. If the luminous points be moved aside, so that the images fall on the retina outside the yellow spot, the two luminous points, though at the same distance apart from each other, will give rise to one sensation only, and be seen as one point; they may be moved even farther apart from each other and still give rise to one sensation; and if the two points be placed so much on one side that their respective images fall on the extreme peripheral parts of the retina near the ora serrata, the two images may be separated from each other a very considerable distance and yet give rise to one sensation only. We may vary the experiment by making use of two black dots on a white surface only just so far apart that they can be seen distinctly as two when placed near the axis of vision so that their images fall on or near the fovea, and then, keeping the axis fixed, move the two points outwards, so that their images travel outwards from the fovea; it will be found that the two soon appear as one. The two sensations become fused, as they would do if brought nearer to each other in the centre of the field. The farther away from the centre of the field, the farther apart must two points be in order that they may be seen as two.

It is obvious that the more sharply we can distinguish the several sensations produced by the images of the several points of which any external object may be supposed to be made up, the more distinct will be our vision of the object. In the fovea centralis our power of thus distinguishing sensations is at its maximum; in the outer parts of the yellow spot around the fovea it is less; just outside the yellow spot it is much less; and thence diminishes more gradually towards the periphery of the retina. Hence we speak of the fovea centralis, including more or less of the whole yellow spot, as the "region of distinct vision;" and when we wish to examine closely the features of an external object, we so direct the eye, we so 'look' at the object, that its image falls as far as possible on the fovea centralis. The diminution of distinctness does not take place equally from the centre to the circumference along all meridians. The outline described by a line uniting the points where two spots at a certain distance apart cease to be seen as two when moved along different radii from the centre, is a very irregular figure; it differs very much in different individuals; is often not the same in the two eyes of the same person, and does not necessarily correspond to the figure of "the field of vision" to which we shall later on refer. We may add that the power of distinguishing two points in the peripheral parts of the retina is much increased by practice.

As we have just said, when we look intently at an object such as a star in the heavens we so direct the eye that the image of the object falls on the fovea centralis. In the case of most people, two stars so looked at appear to become one when the angle subtended by the distance between them becomes less than 60 seconds or one minute; when they are nearer than this the two sensations become one. And similar measurements are obtained when other images are made to fall on the fovea, such as those of parallel white streaks on a black ground or black streaks on a white ground. In the case of an acute and trained observer this minimum distance may be diminished to 50 seconds; in many cases, on the other hand, it is not less than 73 seconds and may be more. Now the distance between two points subtended by an angle of 50 seconds corresponds in the diagrammatic eye (§ 705) to a distance of 3·65 $\mu$ in the retinal image, and one of 73 seconds to 5·36 $\mu$. Hence in the fovea centralis the elements of the retina excited by light must lie 3·65 $\mu$ or 5·36 $\mu$ apart, or in round numbers about 4 $\mu$ apart, in order that the two sensations, excited at the same time, may remain distinct. In the ordinary method of testing, visual acuity is said to be normal when the letters used subtend an angle of five minutes, each of the component parts of the letter subtending an angle of one minute.

In the periphery of the retina the distance must be much greater; thus at the extreme periphery, two black dots distant apart about 15 mm. viewed at a distance of 20 cm., and therefore giving a distance of more than a millimeter in the retinal image, are still seen as one point.

This power of distinguishing two sensations is something different from the absolute appreciation of a stimulus, from absolute sensitiveness. In this respect the fovea is inferior to other parts of the retina; it is not so sensitive as they to feeble light. Astronomers have found that stars of low magnitude may be seen better by indirect vision, and experiment has shewn that the fovea is less sensitive to feeble light stimulation than the surrounding parts of the retina. The inferiority of the fovea in this respect is emphasised in the dark-adapted eye; the fovea appears not to partake, or to partake very slightly, in the increase of sensitiveness which follows exclusion of light from the eye.

§ **754.** In accordance with the above, we may suppose the retina to be divided into areas, stimulation of the retina within which gives rise to a single sensation; we might speak of these as visual areas, and of the stimulation of a visual area as a sensational unit. The areas are very small, and the sensational units very numerous, in the fovea centralis and yellow spot; the areas are larger, and the sensational units fewer, over the rest of the retina, increasingly so towards the periphery. The smaller or larger the areas, the more numerous or fewer the sensational units in any retina or in any part of a retina, the more or less distinct will be the vision.

Now in the human eye 50 cones may be counted along a line of 200 $\mu$ in length drawn through the centre of the yellow spot; this would give 4 $\mu$ for the distance between the centres of two adjoining cones in the yellow spot, the average diameter of a cone at its widest part being here about 3 $\mu$, and there being slight intervals between neighbouring cones. Hence if we take the centre of a cone as the centre of an anatomical retinal area, these anatomical areas correspond very fairly in the region of distinct vision to the physiological visual areas just spoken of. If two points of the retinal image are less than 4 $\mu$ apart, they may both lie within the area of a single cone; and it is just when they are less than about 4 $\mu$ apart that they cease to give rise to two distinct sensations. It must be remembered, however, that the fusion or distinction of the sensations is ultimately determined by the brain. The retinal area must be carefully distinguished from the sensational unit, for the sensation is a process whose arena stretches from the retina to certain parts of the brain, and the circumscription of the sensational unit, though it must begin as a retinal area, must also be continued as a cerebral area, the latter corresponding to, and being as it were the projection of, the former. Two points of the retinal image less than 4 $\mu$ apart might lie both within the area of a single cone; but the reason why, under such circumstances, they give rise to one sensation only is not because one cone fibre only is stimulated. For, two points of a retinal image might lie, one on the area of one cone and another on the area of an adjoining cone, and still be less than 4 $\mu$ apart; in such a case two cone fibres would be stimulated; and yet only one sensation would be produced.

In the case where the two points lie entirely within the area of a single cone, it is exceedingly probable that, even if the adjacent cones or cone fibres in the retina are not at the same time stimulated, impulses radiate from the cerebral ending of the excited cone into the neighbouring cerebral endings of the neighbouring cones; in other words, the sensation-area in the brain does not exactly correspond to and is not sharply defined like the retinal area, but gradually fades away into neighbouring sensation-areas. We may imagine two points of the retinal image so far apart that even the extreme margins of their respective cerebral sensation-areas do not touch each other in the least; in such a case there can be no doubt about the two points giving rise to two sensations. We might, however, imagine a second case where two points were just so far apart that their respective sensation-areas should coalesce at their margins, and yet that, in passing from the centre of one sensation-area to the centre of the other, we should find on examination a considerable fall of sensation at the junction of the two areas; and in a third case we might imagine the two centres to be so close to each other that in passing from one to the other no appreciable diminution of sensation could be discovered. In the last case there would be but one sensation, in the second there might still be two sensations if the marginal fall were great enough, even though the areas partially coalesced.

That the ultimate differentiation of the sensations rests with the brain is still more clear in the case of sensations started in the periphery of the retina; two points of a retinal image might stimulate two cones a considerable distance apart, or several cones, to say nothing of the intervening rods, might be stimulated, and yet one sensation only result.

Thus, the distinction or fusion of visual sensations is ultimately determined by the disposition and condition of the cerebral centres. Hence the possibility of increasing by exercise the faculty of distinguishing two sensations, since by use the cerebral sensation-areas become more and more differentiated, though the mosaic of rods and cones fixes for the power of discrimination of each individual a limit beyond which exercise cannot carry improvement. This effect of exercise is however shewn in touch even more strikingly than in sight.

## SEC. 8. ON COLOUR SENSATIONS.

§ **755**. The sensation excited by a luminous point possesses still another character besides those of intensity, duration, constancy, and localisation, namely the one which we speak of as colour.

When we allow sunlight reflected from a white cloud or from a sheet of white paper to fall into the eye, we have a sensation which we call that of white light. When we look at the same light through a prism and allow different parts of the spectrum to fall in succession into the eye, we have a series of sensations, differing in character from the sensation of white light and from each other; these we call 'colour sensations,' sensations of red, yellow, and the like. In the latter case the luminous undulations are dispersed in a linear series according to their wave-lengths, from the short waves of the extreme violet to the long waves of the extreme red; and we learn from the spectrum, on the one hand, that undulations having different wave-lengths produce different sensations, and on the other hand that undulations having wave-lengths longer than that of the extreme red, about λ 760[1], or shorter than that of the extreme violet, about λ 390, are unable to excite the retina and are therefore invisible. When we look directly at a white object all this dispersion is absent, and the retina is excited at the same time by undulations of all the above wave-lengths. A sensation of 'colour' then is a sensation evoked by undulations of particular wave-lengths, a sensation of 'white' is the sensation which results when the retina, or a part of it, is simultaneously excited by undulations of all wave-lengths which are able to affect it, that is by the whole visible spectrum. When we diminish the amount of light which is giving us a sensation of "white" this sensation passes into one of "grey," and by progressive diminution we may obtain a series of greys which pass from "white" at one end of the series to another kind of sensation at the other end, which we call "black." By the sensation "black" is not meant absence of sensation, but a special quality of sensation as definite as any other. Sometimes the word 'colour' is confined to the sensations other than those of white and black, sometimes it is used to comprise these two sensations as well.

---

[1] λ signifies a millionth of a millimeter or ·001 μ.

When we examine the spectrum we are able to perceive a very large number of different colours, we experience a multitude of sensations, no two of which are exactly alike. There are certain broad differences which we express by common names, such as red, orange, yellow, and the like. But we can go much further than this. If we take any part of the spectrum, the green for instance, we find that a very slight change in the wave-length produces a change in the character of the sensation. For convenience sake we call a whole group of sensations green; but we are obliged to admit that there are several kinds of green, several distinct kinds of sensations, though we do not possess names for all of them; a trained eye will recognize that within the green of the spectrum, the sensation produced by one part is a different sensation from that produced by an adjoining part differing in wave-length from the former by an exceedingly small amount. The same is the case with other parts of the spectrum. And in general we may say that any change in the wave-length will produce a change in the sensation, so that we might speak of almost each wave-length as producing a separate sensation.

On the other hand, we also easily recognize that the sensations produced by the spectrum are not all wholly unlike, that some are allied to others, and that in some cases one sensation is intermediate between two other sensations and partakes of the nature of both. We recognize the sensation produced by the part of the spectrum lying between the green and the yellow as partaking on the one hand of the nature of the sensation of green and on the other hand of yellow, and call it yellowish green or greenish yellow; we similarly recognize a greenish blue or a blueish green, and so on. This suggests that our colour sensations are in reality mixed sensations, that the multitude of different sensations to which the spectrum gives rise are brought about not by each wave-length giving rise to a separate and independent sensation, but by means of a certain smaller number of primary sensations excited in different degrees by different wave-lengths and mixed in various proportions.

§ **756**. This view is confirmed when we study in a systematic manner the results of mixing or fusing together colour sensations.

The best method of fusing colour sensations is that of allowing two different parts of the spectrum to fall on the same part of the retina at the same time. We may make use of surfaces coloured with pigments, but in doing so we must bear in mind the nature of the colour of pigments. A pigment possesses colour because when white light falls upon it some of the rays are absorbed while others are reflected. Thus gamboge absorbs the blue rays very largely as well as to a slight extent the red rays, but reflects the yellow rays and with these many of the green rays; indigo on the other hand absorbs the red and yellow but reflects the blue and a good deal of the green. Hence when we look at a yellow gamboge patch our retina is excited not by those rays alone which form the yellow of the spectrum, but by many other rays as well; the colour is not a 'pure' colour, does not correspond to one of the colours of the spectrum, but is a mixture of more than one. And this is the case with most pigments; hence when they are employed in experiments on the mixture of sensations, difficulties and even errors arise which are avoided by the use of the colours of the prism. We may here incidentally remark that mixing the sensations excited by looking at pigments gives very different results from mixing the pigments themselves. Thus when gamboge and indigo are mixed the mixture is green because the gamboge absorbs the blue and the indigo absorbs the red and yellow, while both reflect the green. We shall see presently that when the sensation excited by gamboge is mixed with the sensation excited by indigo the result is a sensation not of green but of white; and we shall see why this is. What we have just said with regard to surfaces coloured with pigments applies also to glasses stained with pigment, it being understood that the colour of stained glass, seen as a transparent object, corresponds to the rays which it does not absorb. When pure pigments, *i.e.* pigments corresponding as closely as possible to the prismatic colours, are used, satisfactory results may be gained, either by using the reflected image of one pigment, and arranging so that it falls on the retina at the same spot as the direct image of the other pigment, or by allowing the image of one pigment to fall on the retina before the sensation produced by the other has passed away. The first result is easily reached by the simple method of placing two pieces of coloured paper a little distance apart on a table, one on each side of a glass plate inclined at an angle. By looking with one eye down on the glass plate the reflected image of the one paper may be made to coincide with the direct image of the other, the angle which the glass plate makes with the table being adjusted to the distance between the pieces of paper. In the second method, the 'colour top' is used; sectors of the colours to be investigated are placed on a disc made to rotate very rapidly, and the image of one colour is thus brought to bear on the retina so soon after the image of another that the two sensations are fused into one.

By these means matches may be made between two mixtures both of pigment and spectral colours. Thus two or more colours may be combined so as to appear indistinguishable from a single colour or from another combination, and such a match is often spoken of as a colour equation.

§ **757.** When in such a colour equation sensations corresponding to the red and yellow of the spectrum are mixed together in certain proportions the result is a sensation of orange, quite indistinguishable from the orange of the spectrum itself. Now the latter is produced by rays of certain wave-lengths, whereas the rays of red and of yellow are respectively of quite different wave-lengths. The orange of the spectrum cannot be made up by any mixture of the red and the yellow of the spectrum in the sense that the red and yellow rays can unite together to form rays of the same wave-lengths as the orange rays; the three things are absolutely different. It is simply the mixed sensation of the red and yellow which is indistinguishable from the sensation of orange; the mixture is entirely and absolutely a subjective one. In the same way we may by appropriate mixtures produce the sensations corresponding to other parts of the spectrum. Now we must suppose that rays of different wave-lengths affect the retina in different ways and so give rise to different visual impulses, that, for instance, the visual impulses generated by orange rays are different from those generated by red rays or by yellow rays. Hence we are led by the fact of mixed sensations being identical with other apparently simple sensations to infer that the visual impulses and hence the visual sensations which any ray originates are of a complex character. We conclude, for instance, that the impulses which a ray in the middle of the orange gives rise to are not simple impulses answering exclusively to the colour of that ray, but complex impulses, parts of which may be excited by rays other than the particular orange ray in question. In saying this we must bear in mind that we possess no direct information of the nature of visual impulses, our knowledge of these being limited to what we learn through the sensations to which they give rise; the complexity of the sensation may be, and indeed probably is, of a different order from that of the visual impulse; to this point we shall return.

The view that our ordinary colour sensations are mixtures of simpler sensations is further confirmed by an examination of the colours of external nature. For, though we see around us very many colours besides those present in the spectrum, yet we find that the sensations of all these colours may be reproduced by mixtures of sensations excited by various parts of the spectrum. Thus the colour purple, which is so abundant in the external world and yet so conspicuous by its absence from the spectrum, may be at once reproduced by fusing in proper proportions the sensations of red and of blue. And very many other colours present in the external world but not seen in the spectrum itself may be produced by mixing various spectral colours in various proportions.

Other colours in nature may be reproduced by mixing spectral colours with white or with black. When by means of a slit we allow a certain limited part of the spectrum, say in the green, to fall on a certain area of the retina, the rays exciting that area have certain wave-lengths, lying within certain limits, say from λ 525 to λ 535; no rays but these are affecting the retina at the time, and the result is the sensation which we call spectral green.

But we might easily so arrange matters that a certain amount of white light, that is of light of all wave-lengths of the visible spectrum, should fall on the area in question at the same time that the green is falling upon it; the result would be a mixed sensation, a sensation of spectral green mixed with the sensation of white, and we should recognize this sensation as different from the sensation of spectral green. Further, by varying the proportion of white to green falling on the area in question at the same time we should have a whole series of different sensations from a green in which there was hardly any white to a white in which there was hardly any green. In such a series of colour sensations we recognize a hue supplied by the spectral colour, and we use the phrase more or less "saturated" to express the proportion of white light; when very little white is present, we speak of the colour as being highly saturated. It need hardly be said that not only individual spectral colours, but all mixtures of these also, may be thus "mixed with white."

Again, taking a given area of the retina we may, on the one hand, throw on to the area a small amount of a spectral colour in such a way that all the elements of the retina in the area are excited, to a slight degree, giving rise to a feeble sensation of that colour; but we may, on the other hand, so scatter a few rays over the area that while some elements are excited others remain at rest and yet in such a way that the excitation of the whole area still gives rise to one sensation only. We may speak of each of these sensations as one in which the sensation of the spectral colour is mixed or fused with the sensation which we call black; or we may distinguish the former as merely a feeble sensation and the latter as more strictly mixed with black. Many of the colours of the external world are of this nature; thus the colours which we call "browns" are mixtures of yellow or of red or of both (and possibly of other spectral colours also) with more or less black. In a similar way we may mix, not a spectral colour, but white with black, various mixtures forming various "greys."

§ **758.** Putting aside these more or less peculiar cases of mixture with black, we may say that the character of a colour depends (1) on the wave-lengths of the particular rays which, either alone or in excess of other rays, are falling on a given area of the retina; (2) on the amount of this coloured light falling on that area in a given time; and (3) on the amount of white light falling on that area at the same time. The first determines what we call the hue, the second the intensity, and the third the amount of saturation. Our common phrases do not distinguish with sufficient accuracy these three conditions, which obviously may exist under various combinations. On the one hand we frequently use wholly unlike names for colours which differ only in degree of saturation, such as carmine and pink; on the other hand we often use the same adjectives for quite different conditions. It is desirable to employ the word 'pale,' to mean little saturated, largely mixed with white, and the word 'deep' or 'rich' to mean highly saturated, slightly mixed with white. The word 'tint' might be used to express various degrees of saturation, the word 'hue' being reserved to denote the dominant wave-length. 'Tone' is frequently employed to express variations of wave-length within a named colour, as for instance different tones of red. The word 'bright' is often used somewhat loosely, but it is desirable to employ it exclusively as identical with 'luminous,' that is to say, as indicating the intensity of the sensation; a colour is more or less bright according to the amount of luminous energy which is being expended on the retina. We may remark, in passing, that while we can easily compare the brightness or luminosity of two white lights or of the same part of the spectrum under a feeble and under a strong illumination, we may feel some difficulty in comparing the amount of brightness of one colour with that of another, the brightness for instance of a given yellow with that of a given red. Conversely the word 'dark' is used to denote feeble intensity, or admixture with black. Lastly, our appreciation of the colours of external objects is modified by the nature of the surface which is coloured, and features so arising receive various names; but these are in reality outside actual colour sensations.

§ **759.** Admitting that our colour sensations may be considered to be much fewer in number than those which we appear to have when we look on the colours of the spectrum or of nature, admitting that rays of light awake in us certain "primary" colour sensations, which mixed in various proportions reproduce all our colour sensations, we have now to ask the question, What is the nature or what are the characters of these primary colour sensations?

In view of the answer to this question we must call attention to certain results which may be obtained by a further study of the mixing of colours, meaning by that the mixing of colour sensations.

We have seen that all the colours of the spectrum mixed together make white. We have now to add that white may also be produced by mixing two colours only, provided that these are properly chosen. If we take a part of the red of the spectrum, and by any of the methods given in § 756 mix it with successive parts of the spectrum, we shall find that the mixture with a particular part of the blue green gives white. These two colours are said to be *complementary* to each other. In order to get a complete white, that is a white free from all colour, a certain proportion between the relative amounts of red and blue green light, that is to say between the intensities of the two sensations, must be observed. And it will be understood that the white thus produced by two small parts of the spectrum is not equal in intensity to the white which would be produced by the combined effect of the whole of the same spectrum. The following may be taken as characteristic complementary colours, the respective wave-lengths being given:

| | |
|---|---|
| Red, λ 656, | Blue Green, λ 492, |
| Orange, λ 608, | Blue, λ 490, |
| Gold Yellow, λ 574, | Blue, λ 482, |
| Yellow, λ 567, | Indigo-blue, λ 464, |
| Greenish Yellow, λ 564, | Violet, λ 433. |

It will be understood that the above are not the only complementary colours; as we pass from the red end of the spectrum towards the green, each successive part of the spectrum has its complementary part on the other, blue side of the spectrum, each wave-length on the red side has its complementary wave-length on the blue side. When we reach the greenish yellow at λ 564, the complementary colour is on the very margin of the violet end of the visible spectrum. But we may go, so to speak, outside the spectrum, for the green of the spectrum has for its complementary colour, purple. Or, to put it in another way, while each end of the spectrum has its complementary colour at the other end, the complementary colour of the middle of the spectrum is a combination of the two ends.

The bearing of these facts on the theory of primary colour sensations is obvious. Two complementary colours excite between them all the primary sensations which are excited by white light, though not to the same intensity. Rays of the wave-length λ 656 falling on the retina give rise to the sensation which we denote as a particular kind of red; they do this, however, not by the simple and exclusive stimulation of a particular red sensation, but by exciting all the primary sensations which are not excited by the wave-length λ 492. Conversely rays of the wave-length λ 492 produce the sensation of blue green by exciting all the primary sensations which are not excited by λ 656. Similarly complex is the effect of other wave-lengths. We may roughly describe each of two complementary wave-lengths as stirring up about half the whole of the primary sensations which can be excited by rays of all wave-lengths.

§ **760**. To produce white out of two colours, out of two parts of the spectrum, we are limited to certain pairs; if we take one colour, we are limited to one other colour, to its complementary; we have no choice. If however we are allowed three colours instead of two, we have a much greater range. If we take any three colours, provided only that they lie a certain distance apart along the spectrum, we can produce white by mixing them in certain proportions. If we take any red, green, and blue, we can by adjusting the amount of each, that is the intensity of each, produce white.

We may go further than this. By adjusting the amounts of each of the three colours we can reproduce all the colours of the spectrum. ' If we take, for instance, a red of a certain wave-length, a green of a certain wave-length, and a blue of a certain wave-length, we can, without calling to our aid any other wave-lengths, by varying the relative intensities of the three, produce not only white light, but also orange, yellow, and violet, with all the intermediate tints, that is to say, produce all the colours of the spectrum; and we may in the same way produce the non-spectral purple. Our choice however is to a certain extent limited; the three colours which we choose must be spread over the spectrum, for we cannot obtain these results with three colours taken from the red and yellow alone, or from the green and blue alone. Moreover, the result is not a complete one; the colour which we thus produce by combining three spectral colours differs from a true spectral colour in not being saturated; it is "mixed with white," more so in some cases than in others; in relation to this deficiency of saturation, the green region of the spectrum behaves differently from the red end and the blue end.

§ **761**. These results shew that the primary colour sensations out of which our recognized colour sensations originate, may be reduced to three in number. If we suppose that we possess three primary sensations so disposed in reference to the spectrum, so arranged so to speak along the spectrum, that a ray of light affects each of the three differently according to its wave-length, we can understand how all our multitudinous colour sensations may arise from the varied excitation of these primary sensations. There may be more than three of these primary sensations, but if so they must behave as if they were three; they cannot be less, since as we have seen the results of mixing two sensations only are extremely limited. We may therefore speak of our vision as *trichromic,* as based on three, or the equivalent of three, primary sensations.

When we attempt to inquire further into the nature of these primary sensations, we find ourselves in the face of two rival theories.

The one, propounded by Young but more fully elaborated by Helmholtz and Maxwell, and known as the Young-Helmholtz theory, teaches that there are three and only three such primary sensations. As we have just seen, any three parts of the spectrum, with certain restrictions, might be chosen as corresponding to these three primary sensations so far as concerns the reproduction, by means of them, of all other colour sensations; hence in determining the nature of the primary sensations we must have recourse to other considerations. We may for instance very naturally suppose that two of the three correspond to the two ends of the spectrum, and may therefore be spoken of as more or less closely corresponding to our recognized sensations of red, and of violet. If red and violet be thus two of the sensations the third one must correspond to green, for only a sensation corresponding to green would give white when mixed with the other two sensations. Or again, choosing green in the first instance as one of the primary sensations for the reason that it stands apart from the others in its complement, purple, not being a spectral colour, we may decide that the two other primary sensations ought to differ as much as possible from each other, and therefore choose red and blue rather than red and violet, since violet is obviously more allied to red than is blue; indeed we may perhaps regard violet, on account of its relations to red, as the beginning of a second spectrum the greater part of which is invisible. The decision between these two forms of the same theory rests on a number of considerations, into the discussion of which we cannot enter here. Unless we specially call attention to the difference between them, which acquires importance on certain occasions only, we shall treat them as identical, and use the words blue and violet in this connection indifferently.

Such a view of three primary colour sensations is represented in the diagram (Fig. 155). Thus the red primary sensation, excited to a certain extent by the rays at the extreme red end, is most powerfully affected by the rays at a little distance from that end, the rays from this point onwards towards the blue end producing less and less effect. The curve of the green primary sensation begins later and reaches its maximum in the green of the spectrum, while the blue or violet primary sensation is still

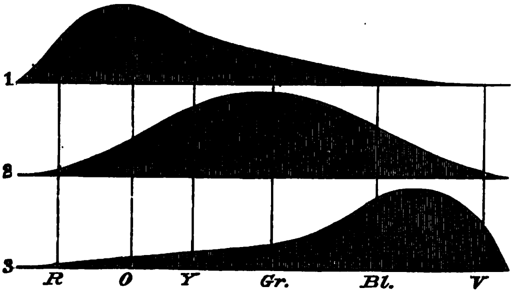

Fig. 155. Diagram of Three Primary Colour Sensations.

1 is the so-called 'red,' 2 'green,' and 3 'violet' primary colour sensation. *R*, *O*, *Y*, &c. represent the red, orange, yellow, &c., colour of the spectrum. The diagram illustrates, by the height of the curve in each case, how the several primary colour sensations are respectively excited to different extents by vibrations of different wave-lengths. But in this, and also in Fig. 156, the curves are to be understood not as careful curves of actual variations in the intensity of the several changes, but as simply serving to illustrate roughly the nature of the theory.

later and only reaches its maximum towards the blue end of the spectrum. Each ray calls forth each primary sensation, though to a different degree, and the total result of each ray, or of each group of rays, is determined by the proportionate amount of the three sensations. Thus the sensation of orange (*O* in the figure) is brought about by a mixture of a great deal of the primary red with much less of the primary green, and hardly any of the primary blue; the orange sensation is converted into a yellow sensation by diminishing the primary red and largely increasing the primary green, the primary blue undergoing also some slight increase. And similarly with all the other sensations. When all the three primary sensations are together excited, each to its whole extent, as when ordinary light falls on the retina, the result is a sensation of white. According to this theory, black is simply the absence of sensation from the visual apparatus.

It will be understood that the pure primary red sensation need not necessarily appear in any of our actual sensations of red; we may suppose that it is always more or less mixed with the primary green and even with the primary blue. So also we may suppose that we never actually experience the primary sensations of green or of blue. Helmholtz finally adopted as the three primary colours a red bluer than spectral red, a green lying between 540 λ and 560 λ, and a blue at about 470 λ, all, however, much more highly saturated than any colours existing in the spectrum.

In this view, as originally put forward by Young, the three primary sensations were supposed to be represented by three sets of fibres, each set of fibres being differently affected by different rays of light, and the impulses passing to the brain along each set awakening a distinct sensation. No such distinction of fibres can be found in the retina; but an anatomical basis of this kind is not necessary for the theory; we can easily conceive of the same fibre transmitting three distinct kinds of impulses; and indeed, as we shall see later on, there are more ways than one by which we can imagine the sensations to be differentiated.

§ **762**. Another theory, that of Hering, starts from the observation that when we examine our own sensations of light we find that certain of these seem to be quite distinct in nature from each other, so that each is something *sui generis*, whereas we easily recognize all other colour sensations as various mixtures of these. Thus red and yellow are to us quite distinct: we do not recognize any thing common to the two; but orange is obviously a mixture of red and yellow. Green and blue are equally distinct from each other and from red and yellow, but in violet and purple we recognize a mixture of red and blue. White again is quite distinct from all the colours in the narrower sense of that word; and black, which we must accept as a sensation, as an affection of consciousness, is again distinct from everything else. Hence the sensations, caused by different kinds of light or by the absence of light, which thus appear to us distinct, and which we may speak of as 'native' or 'elementary' sensations, are white, black, red, yellow, green, blue. Each of these seems to us to have nothing in common with any of the others, whereas in all other colours we can recognize a mixture of two or more of these.

This result of common experience suggests the idea that these elementary sensations are the primary sensations, concerning which we are inquiring. And Hering's theory attempts to reconcile, in some such way as follows, the various facts of colour vision with the supposition that we possess these six fundamental sensations. The six sensations readily fall into three pairs, the members of each pair having analogous relations to each other. In each pair the one colour is complementary to the other; white to black, red to green, and yellow to blue.

The little we know about the actual nature of sensations leads us to believe that the nervous processes which are at the bottom of sensations are, like other nervous processes, the outcome of metabolic changes in nervous substance. We shall presently call attention to the view that vision originates in the metabolic changes of a certain substance (or substances) in the retina, that the metabolism of this substance, which has been called visual substance, is especially affected by the incidence of light, and that the metabolic changes so induced determine the beginnings of visual impulses and thus of visual sensations. In the metabolism of living substance, we recognize (§ 30) two phases, the upward constructive anabolic phase, and the downward destructive katabolic phase; we may accordingly, in the absence of any distinct leading to the contrary, on the one hand suppose that different rays of light, rays differing in their wave-length, may affect the metabolism of the visual substance in different ways, some promoting anabolic, others promoting katabolic changes, and on the other hand that different changes in the metabolism of the visual substance may give rise to different sensations. We say 'in the absence of distinct leading to the contrary,' because though in our study of muscular contraction we were led to regard the effect of a stimulus as a katabolic one, as of the nature of an explosive decomposition, we cannot take a muscular contraction as the exclusive type of the effect of a stimulus; and indeed even in the case of muscular tissue we saw, in the instance of the augmentor and inhibitory cardiac nerves, that nervous impulses, in acting as stimuli, might have contrary effects, effects moreover suggesting that the one, augmentor, were associated with katabolic and the other, inhibitory, with anabolic changes. In all probability, we ought to regard the study of sensations as more likely to throw light on the molecular changes involved in muscular contraction, than to take the little we know about the latter as a guide to our views concerning the former.

We may therefore regard ourselves as at liberty to suppose that there may exist in the retina a visual substance of such a kind that when rays of light of certain wave-lengths, the longer ones for instance of the red side of the spectrum, fall upon it, katabolic changes are induced or encouraged, while anabolic changes are similarly promoted by the incidence of rays of other wave-lengths, the shorter ones of the blue side. But, as we have already said, it is difficult in these matters of sensation to distinguish between peripheral, retinal, and central, cerebral events; we may accordingly extend the above view to the whole visual apparatus, central as well as peripheral, and suppose that when rays of a certain wave-length fall upon the retina, they in some way or other, in some part or other of the visual apparatus, induce or promote katabolic changes and so give rise to a sensation of a certain kind, while rays of another wave-length similarly induce or promote anabolic changes and so give rise to a sensation of a different kind.

The theory of Hering, of which we are now speaking, applies this view to the six fundamental sensations, and supposes that each of the three pairs is the outcome of a particular set of

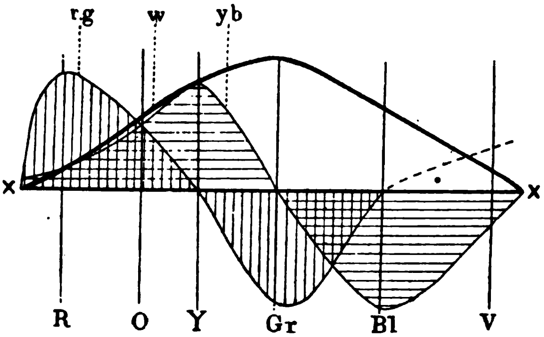

FIG. 156. DIAGRAM TO ILLUSTRATE HERING'S THEORY OF COLOUR VISION.

The lines *R.O.Y.Gr.Bl.V.* indicate, as in Fig. 155, the position on the spectrum of red, orange, yellow, green, blue, and violet.

The line *r.g.*, which includes a space, shaded vertically, is intended to represent the effect of rays of different wave-lengths on the red-green visual substance. In the red, orange and yellow up to the line *Y*, the effect is katabolic, one of dissimilation (red sensation). *Y.* marks the position of equilibrium; beyond this the effect is anabolic, one of assimilation (green sensation). Beyond the blue, *B*, the effect (indicated by a broken line) is represented as once more katabolic.

The line *y.b.* similarly represents the behaviour of the yellow-blue substance, shaded horizontally, katabolic (yellow) up to *Gr*, anabolic (blue) beyond.

The line *w.* similarly indicates the white-black substance, unshaded, katabolic (sensation of white) along the whole length of the spectrum.

katabolic and anabolic changes; these we may provisionally speak of as changes in a distinct visual substance, without attempting to decide whether the changes are retinal or cerebral or both. The theory supposes the existence of what we may call a red-green visual substance, of such a nature that so long as its metabolism is normal, katabolic and anabolic changes being in equilibrium, we experience no sensation, but that when katabolic changes (changes of dissimilation, in Hering's own term) are increased, we experience a sensation of (elementary) red, and when anabolic changes (changes of assimilation) are increased we experience a sensation of (elementary) green. A similar yellow-blue visual substance is supposed to furnish through katabolic changes a yellow, through anabolic changes a blue sensation; and a white-black visual substance similarly provides for a katabolic sensation of white, and an anabolic sensation of black. The two members of each pair are therefore not only complementary but also antagonistic. Further, these substances are of such a kind that while the white-black substance is influenced in the same way though to different degrees by rays along the whole range of the spectrum, the two other substances are differently influenced by rays of different wave-length (see Fig. 156). Thus in the part of the spectrum which we call red, the rays promote a large katabolism of the red-green substance with comparatively slight effect on the yellow-blue substance; hence our sensation of red. In that part of the spectrum which we call yellow the rays effect a large katabolism of the yellow-blue substance, but their action on the red-green substance does not lead to an excess of either katabolism or anabolism, this substance being neutral to them; hence our sensation of yellow. The green rays, again, promote anabolism of the red-green substance, leaving the anabolism of the yellow-blue substance equal to its katabolism; and similarly blue rays cause anabolism of the yellow-blue substance, and leave the red-green substance neutral. Finally, at the extreme blue end of the spectrum, the rays once more provoke katabolism of the red-green substance, and by adding red to blue give violet. When orange rays fall on the retina, there is an excess of katabolism of both the red-green and the yellow-blue substance; when greenish-blue rays are perceived there is an excess of anabolism of both these substances; and other intermediate hues correspond to varying degrees of katabolism or anabolism of the several visual substances.

When all the rays together fall on the retina, the red-green and yellow-blue substance remain in equilibrium, but the white-black substance undergoes great katabolic changes; and we say the light is white.

Such are the two main theories of colour vision; and much may be said in favour of both of them; at the same time both of them present difficulties. We may perhaps regard as the distinctive feature of Hering's theory the view that white is an independent sensation, and not, as according to the Young-Helmholtz theory, the secondary result of the mixture of primary sensations. In Hering's theory rays of all wave-lengths (within the range of the visible spectrum) give rise to the sensation of white, whatever may be the colour sensation produced at the same time; a fully saturated colour, one wholly unmixed with white, according to this view does not exist. This assumption enables us to explain much more readily than does the Young-Helmholtz theory the occurrence under certain circumstances of white sensations replacing or accompanying, that is to say diminishing the saturation of, colour sensations. On the other hand it introduces what appears to many minds a grave difficulty in reference to black. The theory supposes that the sensation of black is the result of the predominance of anabolic changes in the white-black substance. But what name are we to give to the sensation when the white-black substance is in a condition of equilibrium? We cannot investigate the corresponding conditions of equilibrium in the red-green, or in the yellow-blue substance, because we can never study these by themselves. When either of them occurs, as when rays limited to certain wave-lengths are falling on the retina, we are by hypothesis at the same time subject to changes in the white-black substance; we may therefore leave these two conditions of equilibrium on one side. But we are constantly experiencing the condition of equilibrium of the white-black substance, unaccompanied by any stimulation of either the red-green or yellow-blue substance; we do so when the influence of light has for some time been wholly removed from the eye, or again taking the view, which is the more probable one, that the changes of which we are speaking are cerebral changes, when the retina by disease or injury has become insensible to light. Under such circumstances we must suppose that the previous katabolic excitement of the white-black substance has died away, and that the substance is in equilibrium. Now when we examine our sensation under these circumstances, we find that though it is one of darkness it is one which differs from a sensation of intense blackness. So distinct is the difference that the sensation in question has been spoken of under the phrase "the intrinsic light of the retina." And that we may experience sensations of black different from this sensation due to the retina being at rest may be shewn in several ways. When we close and shade the eyes after they have been exposed to a very bright sunlight, we first experience a sensation of blackness, but this soon gives way to the sensation of mere darkness corresponding to the "intrinsic light of the retina." Again, if we stare for some time at a white disc on a black field and then close the eyes, what we shall speak of presently as a negative after-image is developed; the part of the field of vision corresponding to the white disc appears as a black disc, which by its blackness stands out in fairly strong contrast to the rest of the field of vision, which corresponding to the area of the retina previously free from the stimulus of light, now yields the sensation of the "intrinsic light of the retina." And other examples of a similar kind might be given. Admitting then that the "intrinsic light of the retina" corresponds to a condition of equilibrium of the white-black substance, we may speak of this as the neutral condition on one side of which we have sensations of white and on the other side sensations of black. Such a neutral condition has been spoken of as a "neutral grey," but the word grey is so often associated with a mixture of white and black sensations coexisting at the same time rather than with a neutral condition, that the term seems unsuitable. Many minds find it difficult to realize that the condition of which we are speaking is a true neutral condition, the various degrees of blackness being insignificant compared with the various degrees of intensity of white, and accordingly find it difficult to accept Hering's theory.

Both theories conform to the conclusion (§ 761) that normal vision is trichromic in the sense of being made up of three factors; for the three pairs of fundamental sensations of the one theory (the two members of each pair being reciprocally antagonistic, the positive and negative phase of the same thing) play the same part in the equations of mixtures as the three primary sensations of the other theory. Indeed it will be found on examination that all the results of the mixtures of colours are equally explicable on both theories. In comparing the two theories, however, especially in reference to the results of mixtures, we must bear in mind that "brightness" or "luminosity" does not possess the same meaning in the two theories. In the Young-Helmholtz theory brightness is dependent on the extent to which the primary sensation is excited, on the amount of energy expended in the physical substratum, whatever that may be, of the primary sensation. The red of the extreme red end of the spectrum has a minimum of brightness since the extreme red rays excite the red sensation to a minimum and the other two sensations hardly or not at all. As we pass bluewards the brightness increases, partly because the red sensation is more powerfully excited, but also because to the brightness of the red sensation there is now added the brightness of the green sensation. And the brightness of a saturated yellow, such as that of the spectrum, is the sum of the brightnesses of the red and green sensations and nothing else; we neglect for the sake of simplicity the minute adjunct of the blue sensation. In Hering's theory the case is different. The lack of brightness at the red end of the spectrum is due not merely to the feeble development of the red sensation, to the feeble (katabolic) excitement of the red-green substance, but also to the feeble development of the white sensation, to the feeble (katabolic) excitation of the white-black substance; and the brightness of the yellow of the spectrum is due not merely to the large development of the yellow sensation but also to the large increase of the white sensation.

We may here remark when the extreme red end of the spectrum is examined it is found that along a certain length, between λ 760 and λ 655, there is no change in the sensation as regards hue but only as regards luminosity; the red remains exactly the same kind of red, it only becomes brighter and more readily seen. Similarly at the other end from λ 430 to λ 390 the sensation of violet remains of the same hue though differing in luminosity. And these facts have been brought forward on the Young-Helmholtz theory in support of violet being a primary sensation; it is urged that the red and violet which thus do not change in hue but only in luminosity correspond to the actual primary sensations. The behaviour at the red end is quite intelligible on Hering's theory, since as the waves shorten in length both the red and the white sensations are supposed to increase, though probably in this part of the spectrum the white sensation is very feeble, rapidly increasing a little farther on. The behaviour at the violet end presents difficulties, since if the violet be due to admixture with a second octave so to speak of red, the violet should change in hue, become more red, as the rays shorten. But the same difficulty presents itself to the Young-Helmholtz theory if blue be accepted as a primary sensation. Moreover observations on this part of the spectrum are exceedingly difficult. We cannot, however, attempt to discuss the contending theories properly; this would carry us beyond the limits of this book. We must content ourselves with incidental reference to some conclusions, which are suggested by the study of some other features of colour sensations as well as of abnormal colour vision, and to these we may now turn.

§ **763.** What we have said concerning colour vision refers to the central parts of the retina only. If a coloured object be moved so that its image travels from the central to the peripheral parts of the retina, the colour sensations change, the peripheral parts being less sensitive to some colours than to others. If colour stimuli of moderate intensity are employed it is found that at the extreme periphery of the retina no colours are recognized; all give sensations of simple luminosity. On passing inwards towards the centre, the first colours to be seen are yellow and blue, and only on getting towards the central region of the retina are red and green recognized. It is said that the limits for yellow and blue coincide with one another if care be taken to make the colours of the same brightness and saturation, and the same is said to be the case for red and green. If however intense colour stimuli are employed, all colours are recognized as such to the extreme periphery. In consequence of these different limits of sensibility for different colours, very striking changes of hue may be seen on passing mixed colours from the periphery to the centre of the field of vision. Thus orange is seen first as grey, then as yellow, and only becomes orange when it enters the region of sensitiveness to red. Similarly purple and blue-green are seen as blue in the periphery, and are only seen in their true colour when they reach the central region. It is further found that there are four colours which do not change in this way; each of them when seen at all appears of the same hue both in the peripheral and central parts of the retina. These four colours are a red obtained by the addition of blue to the red of the spectrum; a yellow of 574·5 λ; a green of 495 λ; and a blue of 471 λ. These colours have been adopted by Hering as the four primary colours of his theory, and it will be noticed that the red and blue correspond with two of the primary colours most recently adopted by Helmholtz.

§ **764.** In the macula lutea, or yellow spot, the yellow pigment which (§ 744) is diffused through the retinal structures in this region absorbs some of the greenish-blue rays of the light which falls upon it. We may use this feature of the yellow spot for the purpose of making the spot, so to speak, visible to ourselves, by the following experiment. A solution of chrome alum, which only transmits red and greenish-blue rays, is held up between the eye and a white cloud. The greenish-blue rays are absorbed by the yellow spot, and here the light gives rise to a sensation of red; whereas in the rest of the field of vision, the sensation is that ordinarily produced by the purplish solution. The yellow spot is consequently marked out as a rosy patch. This very soon however dies away.

Though, when we wish our vision to be most acute, we use the fovea centralis in which the pigment is extremely scanty or absent owing to the thinness or absence of all retinal layers except the cones and cone fibres, still in ordinary vision we make large use of the whole yellow spot, and our sensations of the colour of external objects must be to a certain extent influenced by the pigment of the spot. The light which reaches the rods and cones of this region from objects which we call white, is in reality more or less tinged with yellow; in other words, what we call white is more or less yellow. Indeed variations in the amount of pigment present in the yellow spot have been offered in explanation of some of the differences in colour vision discussed above. As already mentioned (§ 753) the absolute sensitiveness of the fovea is less than that of the rest of the retina.

§ **765.** *Variations in Colour Vision. Colour-Blindness.* Persons differ very much in their power of appreciating and discriminating colours, and that quite independently of their ability to give expression to their colour sensations, that is to say, of their skill in naming colours. One person will regard as identical two colours which another person recognizes as different. In many cases such differences in the power of discriminating colours are slight, but in some cases they are great. Certain persons are met with who regard as quite alike, or nearly alike, colours which to most people are glaringly distinct; such persons are said to be "colour-blind."

The most common token of "colour-blindness" is the inability to distinguish, or the difficulty in distinguishing, red and green. The great chemist Dalton, who was colour-blind, found great difficulty in recognizing at a distance his red (Glasgow) college gown when it was lying on the college grass-plot; the colour-blind can tell a cherry among the leaves on a tree much more by its form than by its colour; and when such persons are asked to 'make matches' between coloured objects, such as skeins of coloured wools, they will put together a red skein and a green skein as being of the same colour. Most colour-blind people more or less confound red and green; but when a number of such colour-blind persons are tested in making matches either between skeins of wool or otherwise, it is found that they do not all make the same matches; they do not agree as to the particular red and green which they regard as identical, and they disagree in various other matches. But they all agree in this that they see the spectrum in two colours only; in one colour from the red end to a point in the blue green, and in another colour from this point to the violet end. At the point of transition lying between 505 $\lambda$ and 492 $\lambda$, there is a region in which no colour can be recognized, which is called the "neutral band." In most cases this region is very narrow and is only clearly marked in a prismatic spectrum of such wide dispersion that there is little overlapping of rays of different wave-length; in other cases, however, it is broader and its existence more easily determined. All the colours which these colour-blind people see may be reproduced by mixing light from any part of the half of the spectrum on one side of the neutral band with light from any part of the other half, and the colour of any part of one half may be matched with any other part of the same half by suitable adjustment of intensity and saturation. The vision of such people is therefore dichromic; all their colour sensations are compounded of two, not three (or two, not three pairs of) primary sensations. Since the characteristic mistake which is made is to confound red and green, this condition may be spoken of as red-green blindness. In addition to complete cases of this kind others are met with in which there is a lesser degree of the defect; red and green are only confused with one another when very dark or of very slight saturation.

On further examination it is found that cases of red-green blindness may be more or less successfully divided into two classes. In one class the spectrum seems to be shortened at the red end; that is to say, they fail to receive any visual sensation from the rays of extremely long wave-length which still give to the normal eye a distinct sensation of red. They confound, as we have said, reds and greens, but when asked to make an exact match between a red and a green they choose a bright red and a dark green. To members of the other class the spectrum is not shortened; they receive sensations as far to the red side as does the normal eye. When asked to make an exact match between red and green they choose a red and a green which are of about equal brightness to the normal eye. It has been stated that the neutral band occupies a different position in the two classes of red-green blindness, but this does not appear to be the case.

§ **766**. The causes of these two kinds of colour-blindness have been differently explained. In accordance with the Young-Helmholtz theory it has been supposed that in one of the two classes of red-green blindness, namely, that in which the spectrum is shortened at the red end, the red primary sensation is absent, and that the two colours in which the spectrum is seen are green and blue. In the other class it has been supposed that the green sensation is absent, the spectrum being seen as red and blue. In consequence these two classes have been called "red-blind" and "green-blind" respectively. It is obvious that what the normal eye calls red is seen by the first class as a dark colour, and by the second class as a bright colour, *i.e.* of the same brightness as to the normal eye. Hence without any reference to theory, the former may be called *scoterythrous*[1] and the latter *photerythrous*[2]. These names, however, should not be taken to imply that either class experience the red sensation of the normal eye, but only that the part of the spectrum which is red to the normal eye is relatively dark to one class and bright to the other.

The phenomena, however, of these two classes of colour-blind eyes can also be interpreted on Hering's theory. In both of them the red-green substance may be supposed to be missing, and their dichromic vision to be made up exclusively of changes in the yellow-blue and white-black substances. Since they are thus supposed to have neither red nor green sensations, they must necessarily confound red and green; and the smaller differences, which, as we have seen, divide into two classes all those which confound red with green, may be explained as follows.

Even in eyes which may be considered normal as regards colour vision, eyes which certainly cannot be called colour-blind, considerable differences will, on closer examination, be found in regard to sensations of yellow. If by means of a special arrangement we bring a certain amount of the red part of the spectrum and a certain amount of the green part of the spectrum on to the eye at the same time, the result is a sensation of yellow; according to the Young-Helmholtz theory yellow is a mixture of red and green. By the same arrangement we can bring on to the eye at the same time a certain amount of the actual yellow of the spectrum. In this way we can make a match between a mixture of spectral red and green on the one hand, and spectral yellow on the other, comparing the mixed sensation derived from two parts of the spectrum with the sensation derived from a single (yellow) part. We have to adjust the quantities of red light and green light until the mixture seems of the same hue and the same brightness as the yellow, not shewing either a reddish or a greenish tone. When this is done it is found that different people differ very materially as to the proportion of red and green, the proportion of the intensities of the two sensations, necessary to make the match with yellow; with the same quantity of red some need more green, others less green, to make the match. This, on the Young-Helmholtz theory, is interpreted as meaning that the development of the red and green primary sensations differs even in people whose colour vision is considered normal. But on Hering's theory, in which yellow is a fundamental sensation, it may be interpreted as meaning that the yellow-blue substance is more affected by red rays in some people than in others. By Hering's hypothesis, cf. Fig. 156, the rays of the spectrum from the red end to the (pure) green acts on the yellow-blue substance in the way of katabolism, and in favour of this view is the fact that the extreme red of the spectrum when isolated has a distinct yellow tinge. If we suppose that in some eyes the yellow-blue substance is more strongly affected by red rays, the red sensation would be mixed with more yellow in some individuals than in others; hence in such eyes a certain amount of red being mixed with more yellow would need less green (with its accompanying yellow) to produce a certain amount of yellow as the result of the mutual neutralisation of the red and green. In such cases we may suppose not that the whole relation of the yellow-blue substance to wave-lengths is altered, but merely that the sensitiveness to long wave-length is increased. Not only this match of red and green with yellow, but other matches of a similar nature, shew that in different eyes the yellow sensation (in Hering's sense) is more prominent in some people than in others, that some people so to speak are more yellow sighted than others, and according to Hering these differences depend on different degrees of pigmentation of the macula and of the lens in different individuals.

---

[1] *σκότος*, darkness, and *ἐρυθρός*, red.

[2] *φῶς*, light, and *ἐρυθρός*.

The application of this fact to colour-blind cases is obvious. In the one class, the red-blind of the Young-Helmholtz theory, the relations of the primary sensations, the distribution along the spectrum of the visual substances are the same as in the normal eye save that the red-green substance and the corresponding sensations are missing; and since the visibility of the red end of the spectrum is chiefly effected by the red sensation, the white-black and yellow-blue substances being as compared with the red-green substance but slightly sensitive to the extreme rays, the spectrum is shortened. The feeble white and yellow visual impulses excited are insufficient to affect consciousness unless supported by red visual impulses. In the second class, the yellow-blue substance has undergone a change similar to but probably greater than that which obtains in the yellow-sighted but otherwise normal eyes mentioned above, it is more sensitive to the rays at the red end of the spectrum; hence the spectrum to eyes of this class seems of the ordinary visible length.

§ **767.** So far then both theories may be made to explain the ordinary phenomena of colour-blindness; but it is obvious that the subjective condition of the colour-blind must be different according to one theory from what it is according to the other. According to the Young-Helmholtz theory the red-blind person does not experience in any degree the sensation of either red or yellow; from the green of the spectrum to the red end he only sees some sort of green. Indeed along the whole spectrum, the sensations which he experiences are only various kinds of green and blue, with various amounts of the sensation whatever it be, whether white or simply green-blue, or some other sensation unknown to the normal eye, which results from the mixture of the green and blue sensations. The green-blind person, according to the same theory, has only the sensations of red and blue, with the sensation whatever it may be derived from the mixture of these two, he never has the sensation of either green or yellow. Obviously the sensations of the two classes ought to differ very widely.

According to Hering's theory, both classes agree in seeing neither red nor green, all their sensations are made up of yellow and blue, with white and black, and the only difference between the two classes is that the one, the green-blind of the other theory, see more yellow than do the other.

We cannot of course tell what are the actual sensations of the colour-blind; no man can tell what are the sensations of his fellow man; but a person who having normal vision in one eye was colour-blind in the other eye could act as an interpreter. Such a case is recorded; and of him it is said that the sensation which he experienced in his colour-blind eye from the red side of the spectrum resembled not the green but the yellow of his normal eye. It is also stated that in the cases in which persons have become colour-blind through disease of the nervous system, the sensations of red and green disappear together and before those of yellow and blue; such persons have the memory of their normal colour sensations for comparison. Moreover intelligent colour-blind persons who have studied their own cases are confident that something corresponding to the yellow sensation of the normal eye enters largely into their vision, and is not, as according to the Young-Helmholtz theory ought to be the case, wholly absent. No great stress of course can be laid on this, but as far as it goes it supports the conclusion that what we can learn about actual subjective conditions is in favour of Hering's theory. We may add that according to Hering's theory we should expect the sensations of the so-called red-blind and green-blind not to be wholly unlike since they differ only in the amplitude of their sensations of yellow, whereas according to the Young-Helmholtz theory they ought to be wholly unlike, since red is wholly unlike green. It is true that when the curves of the red and green primary sensations are carefully worked out they lie much closer to each other than does either to that of the primary blue sensation; but this does not do away with the fact that subjectively the primary sensation of red must be something quite different from that of green. Hence further support is given to the former theory by the fact that while there is no difficulty in finding out whether a person is colour-blind or no, it needs much greater care to determine to which class he belongs; indeed, as seems easy on the one theory, but difficult on the other, cases occur which by different observers are placed now in the one class, now in the other. The condition of the peripheral retina of the normal eye (§ 763) affords further evidence in favour of yellow and blue as the two colours of dichromic vision. There is a very close correspondence between the vision of red-green blindness (especially of the photerythrous group) and the vision of the normal peripheral retina. Colour matches good for one are found to be good for the other, and this correspondence is distinctly in favour of yellow and blue as the subjective colours of dichromic vision and therefore in favour of Hering's theory. There are however some difficulties; differences have been found to exist between the vision of the scoterythrous group and that of the peripheral retina which cannot at present be satisfactorily explained by any theory.

It might appear at first sight that the lack of one or more primary sensations would lead to a general deficiency of vision. But this does not necessarily follow; the two remaining sensations might become more highly developed, might so to speak expand in the absence of the others. And as a matter of fact the general vision of colour-blind people seems to be as good as that of normal eyes; moreover, within the range of the colours which they can see, colour-blind people are if anything more acute than most people; though they regard as more or less alike two colours which seem to the normal eye wholly unlike, they can more easily detect minute differences, such as those of shade or tone, within each of the two colours.

§ **768.** We have treated of the colour-blind as if they were confined to those who confounded red with green, but people have also been found who confuse yellow and blue. Such cases are very rare and in those most fully investigated there has also been a partial defect of vision for red and green. The blue end of the spectrum is shortened and there is a neutral band in the yellow region. According to the Young-Helmholtz theory such individuals lack the blue or violet sensation and have therefore been spoken of as "blue-blind or violet-blind." In accordance with Hering's theory the condition has been called "yellow-blue blindness," the yellow-blue substance being supposed to be missing. The drug santonin has also been said to produce violet-blindness; the effect of the drug is first to excite sensations of violet, and then annul them; but careful observations shew that vision under the influence of santonin is not truly dichromic and that the effects of the drug therefore are not due to its abolishing a primary sensation. We may add that the peculiar effect of the drug is not due to any coloration of retinal structures, but appears to be the result of cerebral or at least of central changes.

Lastly we may remark that total colour-blindness, a condition in which shades of black and white alone indicate the features of external objects, while possible on Hering's theory, is impossible on the Young-Helmholtz theory. According to the latter a person reduced to one primary sensation must see either red, green, or blue; this one sensation is excited in him both by objects which we call coloured and by objects which we call white. He would probably call it white; but it would be either red, green, or blue. According to Hering's theory he might still see white and black in the total absence of both the red-green and the yellow-blue substance. Numerous cases have now been described in which this defect exists. All colours are confused, and any one part of the spectrum may be matched with any other by simple adjustment of intensity. The spectrum is seen as a band of light of which the different parts differ only in luminosity. The point of the spectrum which appears the brightest is not, as in the normal eye, in the yellow but in the part which to the normal eye appears green, at or near the line *E*. The red end is shortened and is relatively much darker than to the normal eye. These cases might indeed be reconciled to the Young-Helmholtz theory by help of the supposition that in such a case the primary sensations were not wanting, but shifted so to speak in their relative positions along the length of the spectrum, brought into the same position on the spectrum, so that each ray of light affected them all equally; or, what amounts to the same thing put in another way, that in such a case there had been a return to a primitive condition, in which light produced one kind of visual sensation only, not yet differentiated into colour sensations. But such a supposition in laying one difficulty would raise many others.

§ **769**. In speaking of the relation between a visual sensation and the intensity of the stimulus (§ 747) we were confining our remarks to white light; when we inquire into the behaviour of our colour sensations under variations in the intensity of the stimulus, we come upon results which are in many ways complicated. We must be content with pointing out one or two only of these.

Each of our colour sensations, when the light giving rise to it reaches a certain intensity, ceases to be a colour sensation and becomes a sensation of white. The theory of three primary colour sensations may be used to explain this. Thus, taking violet as a primary sensation, a violet light of moderate intensity appears violet because it excites the primary sensation of violet much more than those of green and red. If the stimulus be increased the maximum of violet stimulation will be reached, while the stimulation of green will continue to be increased and even that of red to a slight degree. The result will be that the light appears violet mixed with green, that is to say, appears blue. If the stimulus be still further increased while the green and violet are both still largely excited the red stimulation may be increased until the result is violet, green, and red in the proportions which make white light. And so with light of other colours. But the same facts may also be explained on Hering's theory, for this supposes that the stock, so to speak, of white-black substance is far greater than that of either of the other two visual substances; hence under violent stimulation the white sensation wholly overpowers any accompanying colour sensation.

Conversely, when the intensity of the stimulus is diminished colour sensations may disappear before all sensation of light is lost. When the light is very dim we cease to recognize the colour of coloured objects though we continue to see the objects. And this is not merely because the white light reflected from the object (and it is through this that we chiefly become aware of the form of an object) is more powerful than the particular rays which give the object colour; since even a saturated colour behaves in the same way. If we stay for some time in the dark, *i.e.* adapt the eye to darkness (§ 747) and then observe any part of the spectrum (except red) with a very feeble illumination, it will appear colourless and can be matched with white light. When this is done it is found that the brightest part of the spectrum is in the green at the line *E*, while the red end of the spectrum is dark and shortened as compared with its appearance at ordinary intensities, the blue end being relatively brighter. In fact, the spectrum under these conditions seems to shew an almost exact correspondence with the spectrum of total colour-blindness. Moreover, the colour which is first recognized upon gradually increasing the illumination, appears less saturated, that is to say apparently more mixed with white than when a large amount of light of the same refrangibility falls on the retina. The alteration of the relative brightness of different parts of the spectrum also shews itself with minor variations in the intensity of the stimulus; we know for instance that when we look at objects in nature under light of varying intensity we find that the colours change unequally as the light diminishes. As is well known the colours of flowers look very different when night is falling from what they do under bright daylight, and we find in particular that in dim lights, as those of evening and moonlight, blues preponderate, reds and yellows being less obvious, whereas in bright lights yellows and reds become prominent.

The colourless spectrum of the dark-adapted eye with feeble illumination is explained by Hering on the assumption that the black-white substance is the only one which is undergoing sufficient change to affect consciousness, the dark-adaptation having greatly raised its sensitiveness while leaving the chromatic substances unaffected; and Hering explains the alteration of relative brightness and the correspondence with the spectrum of total colour-blindness by the assumption that the black-white substance is most strongly affected by the green part of the spectrum, *i.e.* that the maximum of the curve representing the effect of rays of different wave-lengths on the black-white substance is in the green as shewn in Fig. 156. The fact that the place of maximum brightness of the spectrum at ordinary intensities is shifted towards the red end is explained by supposing that red and yellow, the colours due to katabolic activity, have a greater effect on the total brightness of the spectrum than green and blue, due to anabolic activity; in fact, Hering ascribes to the latter a negative effect, and supposes that while the brightness of yellow is due to the action of the black-white substance plus that of the chromatic substances, the brightness of blue is due to the action of the black-white substance minus that of the chromatic substances. The influence of altered illumination is not capable of straightforward explanation on the Young-Helmholtz theory, but, as in the case of total colour-blindness (§ 768) it has been suggested that the three substances are so affected at low intensities that light of any wave-length affects all three equally.

In studying the variations in brightness of different parts of the spectrum it is important to have some measure by means of which to compare two colours in respect of brightness. One method which has been employed is to compare a coloured light with various colourless lights and find that one which seems to be of the same brightness as the coloured light. Everyone knows that the yellow of the spectrum is brighter than the red, and the green brighter than the blue, and similarly it is easy to tell marked differences between a coloured and a white light, but when we have to do with slight differences this method of direct comparison is difficult and open to objection. Of other methods which have been employed, one of the most satisfactory is that of "flicker photometry." The coloured lights to be compared are observed by the method of intermittent stimulation, and the point when flicker passes into a continuous sensation (§ 749) determined for the different colours. For each part of the spectrum a white light may be found which just ceases to flicker with the same interval between the successive stimuli, and by this means a curve of luminosity of the spectrum may be constructed. The brightness of a colour has also been determined by finding the distance at which the colour can only just be recognized, by determining the visual acuity in illumination by that colour, and in various other ways.

There are several other facts of considerable importance bearing on the theory of colour vision, but it will be best to consider these in connection with certain modifications of visual sensations with which we shall have presently to deal. Meanwhile having acquired some general notions of visual sensations, we may turn from the study of the little we know concerning the way in which these sensations originate through retinal changes, to the study of the way in which light falling on the retina gives rise to visual impulses.

## SEC. 9. ON THE DEVELOPMENT OF VISUAL IMPULSES.

§ **770**. We have already called attention to the important fact that the changes which give rise to visual impulses begin on the outer side of the retina, that the rays of light pass through the inner layers of the retina without, as far as we know, producing any effect, and do not begin their work until they reach the region of the rods and cones. It is in this region that the energy of light is transformed into energy of another kind; and the processes here started travel back to the layer of fibres in the inner surface of the retina and thence pass as visual impulses along the optic nerve. That on the one hand the optic fibres themselves are insensible to light, and that on the other hand visual impulses do begin in the region of the rods and cones, is shewn by the phenomena of the blind spot and of Purkinjé's figures respectively.

*The Blind Spot.* There is one part of the retina on which rays of light falling give rise to no sensations; this is the entrance of the optic nerve, and the corresponding area in the field of vision is called the blind spot. If the visual axis of one eye, the right for instance, the other being closed, be fixed on a black spot in a white sheet of paper, and a small black object, such as the point of a quill pen dipped in ink, be moved gradually from the black spot sideways over the paper away towards the outside of the field of vision, at a certain distance the black point of the quill will disappear from view. On continuing the movement still farther outward the point will again come into view and continue in sight until it is lost in the periphery of the field of vision. If the pen be used to make a mark on the paper at the moment when it is lost to view and at the moment when it comes into sight again, and if similar marks be made along the other meridians as well as the horizontal, an irregular outline will be drawn circumscribing an area of the field of vision within which rays of light produce no visual sensations. This is the blind spot. The dimensions of the figure drawn vary of course with the distance of the paper from the eye. If this distance be known, the size as well as the position of the area of the retina corresponding to the blind spot may be calculated from the diagrammatic eye (§ 705). The position thus determined coincides exactly with the entrance of the optic nerve, and the dimensions (about 1·5 mm. diameter) also correspond; the exact size and shape of the blind spot differs however in different individuals. While drawing the outline as above directed the indications of the large branches of the retinal vessels as they diverge from the entrance of the nerve can frequently be recognized. The existence of the blind spot is also shewn by the fact that an image of light, sufficiently small, thrown upon the optic nerve by means of the ophthalmoscope, gives rise to no sensations.

The existence of the blind spot proves that the optic fibres themselves are insensible to light, that light can stimulate them only through the agency of the retinal structures in which they end.

§ **771.** *Purkinjé's Figures.* If one enters a dark room with a candle and while looking at a plain (not particoloured) wall, moves the candle up and down, holding it on a level with the eyes by the side of the head, there will appear in the field of vision of the eye of the same side, projected on the wall, an image of the retinal vessels, similar to that seen on looking into an eye with the ophthalmoscope. The field of vision is illuminated with a glare, and on this the branched retinal vessels appear as shadows. In this mode of experimenting the light enters the eye through the cornea, and an image of the candle is formed on the nasal side of the retina; it is the light emanating from this image which throws shadows of the retinal vessels on to the rest of the retina. In Fig. 158 the light *a* forms an image on the retina at *b*; the light reflected from this spot casts a shadow of the retinal vessel *v* on to another part of the retina at *c*, and the image of this shadow appears in the field of vision at *d*. A far better method is for a second person to concentrate the rays of light, with a lens of low power, on to the outside of the sclerotic where this is thin (§ 712) just behind the cornea; the light in this case emanates from the illuminated spot on the sclerotic and passing straight through the vitreous humour throws a direct shadow of the vessels on to the retina. Thus the rays passing through the sclerotic at *b*, Fig. 157, in the direction *bv*, will throw a shadow of the vessel *v* on to the retina at $\beta$; this will appear as a dark line at B in the glare of the field of vision. This proves that the structures in which visual impulses originate must lie behind the retinal vessels, otherwise the shadows of these could not be perceived.

If the light be moved from *b* to *a*, the shadow on the retina will move from $\beta$ to $\alpha$, and the dark line in the field of vision will move from B to A. If the distance BA be measured when the whole image is projected at a known distance, *k*B from the eye, *k* being the nodal point (§ 705) of the reduced diagrammatic eye, then, knowing the distance $k\beta$ in the diagrammatic eye, the distance $\beta\alpha$ can be calculated. But if the distance $\beta\alpha$ be thus estimated, and the distance *ba* be directly measured, the distances *βv*, *av*, *bv*, *av* can be calculated; and if the appearance in the field of vision is really caused by the shadow of *v* falling on *β*, these distances ought to correspond to the distances of the retinal vessels *v* from the sclerotic *b*, on the one hand, and from that part of the retina *β* where visual impressions begin, on the other. When this is done it is found that the distance *βv* thus calculated corresponds fairly well to the distance of the retinal vessels from the layer of rods and cones. Thus Purkinjé's figures prove in the first place that the sensory impulses which form the commencement of visual sensations originate in some part of the retina behind the retinal vessels, *i.e.* somewhere between them and the choroid coat; and calculations based on the movements of the shadows following movements of the illumination, even if they do not give absolutely exact results, at least go far to shew that these impulses originate at the outermost part of the retina, viz. the layer of rods and cones.

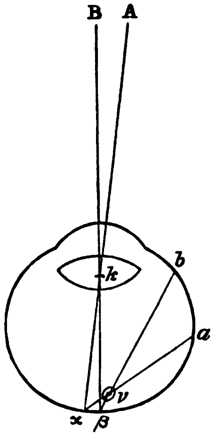

FIG. 157. DIAGRAM ILLUSTRATING THE FORMATION OF PURKINJÉ'S FIGURES WHEN THE ILLUMINATION IS DIRECTED THROUGH THE SCLEROTIC.

In the second method of experimenting, where the light passes through the sclerotic, the image always moves in the same direction as the light, as it obviously must do; when the spot of light on the sclerotic is moved from *a* to *b* (Fig. 157) the shadow on the retina moves from *α* to *β*, and the (inverted) image moves from A to B. In the first method, where the light enters through the cornea, the image moves in the same direction as the light when the light is moved from side to side, provided the movement does not extend beyond the middle of the cornea, but in the opposite direction to the light when the latter is moved up and down. In Fig. 158, which represents a horizontal section of an eye, if *a* be moved to *α*, *b* (the illuminated spot on the retina, the light reflected from which casts a shadow of *v* on to *c*) will move to $\beta$, the shadow on the retina *c* to $\gamma$, and the image *d* to $\delta$. If on the other hand *a* be supposed to move above the plane of the paper, *b* will move below, in consequence *c* will move above, and *d* will appear to move below, *i.e.* *d* will sink as *a* rises.

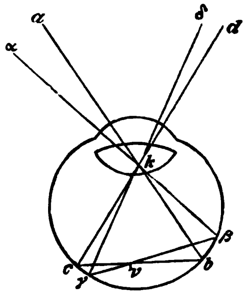

FIG. 158. DIAGRAM ILLUSTRATING THE FORMATION OF PURKINJÉ'S FIGURES WHEN THE ILLUMINATION IS DIRECTED THROUGH THE CORNEA.

It is desirable in these cases to keep moving the light to and fro, especially in the first method, since the retina soon becomes tired, and the image fades away. To give rise to a conscious sensation of the slight difference between shadow and absence of shadow the retina must be extremely sensitive; if the shadow remains motionless, the sensitiveness rapidly decreases in the parts which are not in shadow, until the visual sensations from these parts are no stronger than those from the parts in shadow; when the light is moved the parts which were in shadow, not having been so much stimulated, are sufficiently sensitive to the light which now falls on them, while those parts which had been previously fatigued recover their sensitiveness by resting in the shadow. The experiment, like the experiment by which the yellow spot (§ 764) is made visible, is incidentally useful as shewing how extremely sensitive and how soon fatigued are the retinal structures.

Some observers can recognize in the axis of vision a faint shadow corresponding to the edge of the depression of the fovea centralis.

The retinal vessels may also be rendered visible by looking through a small orifice such as a pin-hole in a card placed close to the eye, in the position of the principal anterior focus, at a bright surface such as a white cloud, and moving the orifice very rapidly from side to side or up and down. If the movement be from side to side, the vessels which run vertical will be seen; if up and down, the horizontal vessels. In this case, as in the similar instance of shadows cast by objects in the vitreous humour (§ 736), the shadow is cast by the rays passing parallel through the vitreous humour; hence the change from shadow to absence of shadow is more marked with the vertical vessels when the movement is sideways, and with the horizontal vessels when it is up and down. The fine capillary vessels are seen more easily in this way than by Purkinjé's method. The same appearances may also be produced by looking through a microscope from which the objective has been removed and the eye-piece only left (or in which at least there is no object distinctly in focus in the field), and moving the head rapidly from side to side or backwards and forwards. Or the microscope itself may be moved; a circular movement of the field will then bring both the vertically and horizontally directed vessels into view at the same time.

§ **772.** It being admitted that the processes which give rise to visual impulses begin somewhere in the region of the rods and cones, we have to ask the question, How do they begin, and what is their nature? We are accustomed to consider light as the undulations of an ether; a nervous impulse is, so far as we can understand, a molecular change propagated along the substance of the axis cylinder of a nerve-fibre; and though, as we have seen, our knowledge of the subject is very limited, still the analogy of a muscular contraction, and of other responses of living substance to a stimulus, lead us to conclude that chemical changes play a part in this molecular change. By what steps does the undulation of the ether give rise to the material molecular change? In attempting to answer this question we may adopt one or other of two views.

On the one hand we may suppose that the vibrations of the ether are able, through the means of the retinal apparatus of the rods and cones for example, to give rise in some more or less direct manner to the molecular vibrations which are the beginnings of the nervous impulses in the optic nerve. And the rapidity with which events must come and go in the retina in order that the eye may be, what it is, an instrument for appreciating rapidly repeated minute changes, lends support to this view. But the present state of our knowledge of physical phenomena does not afford us an adequate explanation of how such a direct transformation can be effected. The recent progress of science tends, it is true, more and more to lay bare the close relations which obtain between optical and electric phenomena, and the latter, as we have so often seen, play an important part in the generation of nervous impulses. Then, again, many of the phenomena of fluorescence seem to supply a bridge between the vibrations of ether and the vibrations of molecules. But in neither of these directions is it possible, at present at all events, to frame a hypothesis which can be satisfactorily applied to retinal processes.

On the other hand we may perhaps more naturally turn to a chemical explanation. We are familiar with the fact that rays of light are able to bring about the decomposition of very many chemical substances; and we accordingly speak of these substances as being sensitive to light. All the facts dwelt on in this book illustrate the great complexity and corresponding instability of the composition of living matter. And we might reasonably suppose that living matter itself would be sensitive to light; that is to say, that rays of light falling on even undifferentiated protoplasmic substance might set up a decomposition of that substance and so bring about a molecular disturbance; in other words, that light might act as a direct stimulus to living matter. As a matter of fact, however, we meet with very little evidence of this, especially when we make a distinction between thermic rays, rays which though they produce physical results are to us invisible, and luminous rays which alone when they fall on our retina give rise in us to the sensation of light. Nor can we be surprised at this apparent indifference of living matter towards light when we reflect that living matter in what we may call its purest form is remarkable for its transparency, that is to say, the rays of light pass through it with exceedingly little absorption. But in order that light may produce chemical effects, it must be absorbed; its energy must be spent in doing the chemical work. Accordingly the first step towards the formation of an organ of vision, that is to say, an organ through which the body of a living being reacts towards light, is the differentiation of a portion of the substance of the body into a pigment at once capable of absorbing light, and sensitive to light, *i.e.* undergoing decomposition upon exposure to light. An organism, a portion of whose body had thus become differentiated into such a pigment, would be able to react towards light. The light falling on the organism would be in part absorbed by the pigment, and the rays thus absorbed would produce a chemical action and set free chemical substances which before were not present. We have only to suppose that the chemical substances thus produced are of such a nature as to induce other chemical changes, or in some way or other to act as a stimulus to other parts of the organism (and we have manifold evidence of the exquisite sensitiveness of living matter in general to chemical stimuli), in order to see how rays of light falling on the organism might excite movements in it, or modify movements which were being carried on, or might otherwise affect the organism in whole or in part. A comparatively simple illustration of this is afforded by some of the lowly organisms called bacteria, especially by the one which has been called *bacterium photometricum.* This organism is remarkably sensitive to light, and especially reacts towards certain rays of light. It is coloured with a purple pigment, apparently allied to chlorophyll; and the rays of light, to which it is especially sensitive, are just those which are absorbed by the pigment.

§ **773**. *Photochemistry of the Retina.* Such considerations as the foregoing may be applied to even the complex organ of vision of the higher animals. If we suppose that the actual terminations of the optic nerve are surrounded by substances sensitive to light, then it becomes easy to imagine how light falling on these sensitive substances should set free chemical bodies possessed of the property of acting as stimuli to the actual nerve-endings and thus give rise to visual impulses in the optic fibres. We say "easy to imagine," but we are, at present, far from being able to give definite proofs that such an explanation of the origin of visual impulses is the true one, probable and enticing as it may appear.

One of the most striking features in the structure of the retina is the abundance of black pigment, fuscin (§ 746), in the retinal epithelium. It is difficult to suppose that the sole function of this pigment is to absorb the superfluous rays of light, and that the rays thus absorbed are put to no use and simply wasted. And indeed it has been shewn that the pigment is sensitive to light; but the changes in it induced by light are excessively slow. Moreover its presence cannot be of fundamental importance, since vision is not only possible but fairly distinct with albinos in which this pigment is absent.

Then, again, in the vast majority of vertebrate animals the outer limbs of the rods are suffused with a purplish-red pigment, the so-called visual purple, which is so eminently sensitive to light that images of external objects may by appropriate means be photographed in it on the retina. When the eye of a frog or of a rabbit is examined in an ordinary way, with full exposure to light, the retina appears colourless. But if the eye be kept in the dark for some time before it is examined, the retina, if removed rapidly, will be found to be of a beautiful purplish-red or pink colour. Upon exposure to light the colour changes to yellow and then fades away. Upon examination with the microscope it is found that the purple colour is confined exclusively to the rods and to the outer limbs of the rods, the inner limbs being wholly devoid of it.

The colour of the rods is due to the presence of a distinct pigment, the "visual purple," diffused through the substance of the outer limbs; and this may be extracted from the rods by dissolving these in an aqueous solution of bile salts. A clear purple solution is thus obtained, which is capable of being bleached by the action of light, and in its general features and behaviour is similar to the pigment as it naturally exists in the retina.

Visual purple is found, as we have said, exclusively in the outer limbs of the rods; it has never yet been found in the cones, and it is accordingly absent from (or exceedingly scanty in) the retinas (such as those of snakes) which are composed of cones only (or contain very few rods), and from the greater part of the macula lutea and the whole of the fovea centralis of the retinas of man and the ape. The intensity of the coloration varies in different animals, and the retinas even of some animals possessing rods seem to be wholly devoid of the visual purple; it is generally well marked in retinas in which the outer limbs of the rods are well developed. Its presence has been found to be in some degree associated with nocturnal habits. It is present in fishes and in most nocturnal animals, in some, as the owl, in great abundance. It has been found almost completely absent however in some bats, but these animals seem to be dependent to a very small degree on vision. Nocturnal animals are also characterised by the external limbs of the rods being very long, thus giving great thickness of the layer of visual purple. It has been found in the retina of the embryo.

The visual purple is bleached not only by white but also by monochromatic light. Of the various prismatic rays the most active are the greenish-yellow rays, those to the blue side of these coming next, the least active being the red. Now it is precisely the greenish-yellow rays which are most readily absorbed by the colour itself. A natural coloured retina or a solution of visual purple gives a diffuse spectrum without any defined absorption bands, and according to the amount of colouring material through which the light passes, absorption is seen either to be limited to the greenish-yellow part of the spectrum or to spread thence towards the blue and, to a much less extent, towards the red. Thus the various prismatic rays produce a photochemical effect on the visual purple in proportion as they are absorbed by it. Under the action of light the visual purple, whether in solution, or in its natural condition in the rods, passes through a purplish orange to a yellow, and finally becomes colourless; and we appear to be justified in speaking of a "visual yellow" and "visual white" as products of the photochemical changes undergone by the visual purple.

For the restoration of the visual purple, after it has been destroyed by light, the maintenance of the circulation of the blood through the tissues of the eye is not essential. The retinal epithelium has by itself, provided that it still retains its tissue life, the power of regenerating the purple. If a portion of the retina of an excised eye be raised from its epithelial bed, bleached, and then carefully restored to its natural position, the purple will return if the eye be kept in the dark.

If the image of some bright object such as a lamp or a window be thrown on to the retina, either of an eye in its natural position or of one recently excised, care having been taken to keep the retina for some time previous away from all rays of light, the portion of the retina on which the rays have fallen will be found to be bleached, the rest of the retina remaining purple. In fact an "optogram" of external objects may thus be obtained; and if the retina be removed and treated with a 4 p.c. solution of potash alum before the retinal epithelium has had time to obliterate the bleaching effects, the retina may remain permanently in that condition: the photochemical effect may, as the photographers say, be "fixed."

It seemed very tempting, especially upon the first discovery of it, to suppose that this visual purple was of great importance in vision. But it is absent from the cones, it is in ourselves absent from the fovea centralis, the region of most distinct vision; it is further entirely wanting in some animals which undoubtedly see very well; and lastly animals such as frogs, naturally possessing the pigment, continue to see very well and even apparently to see colours when their visual purple has been absolutely bleached, as it may be by the prolonged exposure of the eyes to strong light. It is therefore not essential to vision or even to colour vision, but there is much reason to believe that visual purple plays a considerable part in vision with feeble illumination. Its presence and frequent abundance in nocturnal and underground animals first suggested this, and other facts point in the same direction. It seems probable that the great increase of sensitiveness to light, which takes place after staying in the dark, may be due to accumulation of visual purple, and the fact that the fovea does not share in this increase of sensitiveness (§ 764) would be a natural consequence of the absence of visual purple from this part of the retina. The spectrum of the dark-adapted eye is, according to this view, the spectrum of vision with visual purple, and this is supported by the fact that the light which acts most strongly on the dark-adapted eye, viz. yellow-green rays, from the neighbourhood of the line *E* (§ 769) is also that which is most readily absorbed by visual purple. If visual purple is a substance which only comes into play with feeble illumination, it affords an explanation of the fact that in the evening blues become relatively brighter, reds and yellows relatively darker; for visual purple is acted on strongly by blue light, hardly at all by red and yellow light. These changes in the relative brightness of different colours are said not to occur, or to be much less marked, in vision with the fovea alone, from which visual purple is absent.

Another anomaly of colour vision which has been referred to the action of visual purple is the fact that a colour equation (§ 756) made at ordinary luminosities is no longer correct if the illumination is considerably reduced. This phenomenon, which appears to depend on dark-adaptation of the eye rather than on the lowered intensity itself, has been explained by supposing that a new factor, viz. visual purple, which has no appreciable influence at ordinary luminosities, comes into play with feeble illumination. It is further stated that if only the foveal area of the retina is stimulated, this alteration of colour equations does not occur; a match, made in one illumination, holds good in all.

The close correspondence between the spectrum of the dark-adapted eye and that of total colour-blindness (§ 769) has further suggested the idea that in this latter condition, vision depends mainly or altogether on visual purple. This view explains the existence of certain other peculiarities of the vision of total colour-blindness, viz. low visual acuity, and the existence of photophobia in bright light. It has also been found that in some cases of total colour-blindness there is an area of absolute blindness corresponding to the fovea. Rays falling on the fovea produce no visual sensation, those falling on the parts of the retina possessing visual purple produce visual sensations, but these are all alike, that is, devoid of colour.

According to this view visual purple has no direct action in producing colour sensations; but nevertheless, if the view be accepted, the two theories of colour vision do not remain unaffected. The action of visual purple will account for certain anomalous features of colour vision which the Young-Helmholtz theory cannot satisfactorily explain, such as the existence of total colour-blindness and the peculiarities of vision with the dark-adapted eye. There still remain, however, the difficulties connected with the other forms of colour-blindness, and others connected with after-images and contrast which have yet to be considered.

The theory of Hering will also require modification if visual purple acts in the way indicated. According to the theory the vision of total colour-blindness and of the dark-adapted normal eye depends on exclusive action of the black-white substance, but for several reasons this substance cannot be identified with visual purple.

§ **774.** If the eyeball be steadily compressed so as to arrest or greatly interfere with the circulation, the anæmic retina becomes insensitive to light, so that the eye becomes temporarily blind. If while the pressure is being applied the eye is directed to a white and black surface, so arranged that half the field of vision is white and the other half black, that is to say, half the retina is stimulated while the other half is at rest, and if as soon as the white half becomes invisible the black half is made white (by the withdrawal for instance of the black sheet which furnished the black half), then for an instant that new white half becomes visible, though the sensation soon fades away. This result has been interpreted as shewing the existence in the retina of a "visual substance" nourished by the previous blood supply but ceasing to be replenished when the blood supply was interfered with. We may suppose that over the half of the retina stimulated by the light, over the white half of the field of vision, this visual substance was wholly exhausted, while over the half not so stimulated some remained, sufficient to give rise to a fugitive visual sensation when that half was stimulated by light. But the result may be explained without reference to any special visual substance; it is only natural that some part or the whole of the retinal nervous apparatus should be sooner exhausted when stimulation is added to deprivation of nourishment than when stimulation is absent. We may here remark that pressure on the eyeball gives rise to temporary colour-blindness like that existing in the periphery of the retina; as the pressure is continued red and green pass through yellow into white, while yellow and blue pass directly into white.

We have then no satisfactory evidence of the existence of any visual substance or substances, of a photochemical or other nature, lying outside the nervous elements. There may be such, but we have at present no proof of their existence. And it must be remembered, with regard to the hypothetical 'visual substances' of Hering's theory, or of other theories involving the existence of visual substances, that it is not necessary that these should lie outside the nervous conducting elements, or indeed should lie exclusively in the retina. The visual substance is merely supposed to be the basis of visual sensations, it is introduced to explain these sensations; but those sensations are developed in the brain, and as we have already more than once insisted, it is always difficult, and in many cases impossible, to distinguish in a sensation between central and peripheral events. All our knowledge goes to shew that sensations, like other nervous processes, are the outcome of the metabolism of nervous substance; and it is at present quite open to us to suppose that the visual substances, changes in which we recognize as the basis of colour and other visual sensations, are substances forming part of the nervous material of the central organs of vision, each substance being affected in its own way by nervous impulses generated in the retina by rays of light of certain wave-lengths. The various exhaustions, mixtures and the like, supposed by the theories, would on this view take place in the central organ. On the other hand the visual substance may reside in the retina and the central organ may do little more than, so to speak, record the changes which had already taken place in the retina. Or perhaps we ought to make no such sharp distinction between retina and central organ. Our present knowledge is unable to decide these matters; but the acceptance or rejection of the theories of colour vision is quite independent of any view as to the exact nature or position of the visual substances.

An attempt has been made, as by Donders, to reconcile the two theories we have been considering, by supposing that the retinal or peripheral processes are threefold, more or less in the sense of the Young-Helmholtz theory, while the cerebral or central processes are fourfold, and Hering himself is inclined to regard his theory as an expression of central rather than of retinal processes.

§ **775.** Whatever view we adopt, whether photochemical or other, as to the changes which lead to stimulation of the real endings of the retinal nervous mechanism, we cannot at present state anything definite concerning those nerve-endings or the manner of their stimulation.

Each outer limb of a rod is a cylinder of highly refractive material, closely packed round with the black pigment of the retinal epithelium. When an image of an external object, such as a candle-flame, is formed on the retina, at or near the layer of rods and cones, the rays of light diverge again beyond the focal plane in the form of pencils of rays from each point of the image. Of these some passing between the rods are absorbed by the pigment, while others pass into the outer limbs of the rods; of these latter some traversing the whole length of the limb, are absorbed by the pigment beyond, while others undergo "total reflection" at the sides, or are absorbed by the pigment after reflection. Hence of all the rays which fall on the layer of rods and cones, a small number only are reflected back into the vitreous humour and so through the pupil; hence the eye when looked into usually looks black. In the case of the conical outer limbs of the cones the amount of light thus thrown back into the vitreous humour must be still less. We may fairly assume that the light which thus disappears, partly in the actual outer limbs of the rods and cones, partly in their immediate surrounding, sets up changes which, whatever be their exact nature, either are or in some way assist the very beginnings of visual impulses. It also seems probable that these changes, so long as they are confined to the region of the outer limbs, ought not to be considered as nervous in nature, it seems probable that they do not take on a nature analogous to that of a nervous impulse, until they have passed the conspicuous break which divides the outer from the inner limbs. But on these matters we have no certain knowledge.

We may here turn aside for a moment to remark that when an image of a candle-flame is formed on the retina the rays reflected back, as stated above, from the retina through the pupil form a second image in the position of the candle-flame; hence to see an image of an illuminated retina the observing eye must be placed in the position of the source of illumination. This is the principle of the ophthalmoscope.

There are many forms of this instrument, but the accompanying diagram (Fig. 159) will illustrate its essential features. The rays from the lamp *L* (or other source of illumination) are reflected by the concave mirror *M*, *M*, and brought to a focus at *a*. The rays diverging from *a* are, by means of the lens *l*, rendered parallel, and thus, through natural dioptric arrangements of the observed eye *B*, are brought to a focus on the retina at *a'*. The rays reflected back from the part *a'* of the retina thus illuminated, will, as stated above, follow the same path as on entering, and so return to the focus *a*. Hence the rays reflected from a number of points on the retina, such as those forming the arrow at *a′*, will be brought to a focus in a corresponding number of points at *a*, *i.e.* will form an (inverted) image of the arrow at *a*. And the observing eye placed at *A* behind the hole in the mirror will see at *a* an inverted image of the illuminated retina.

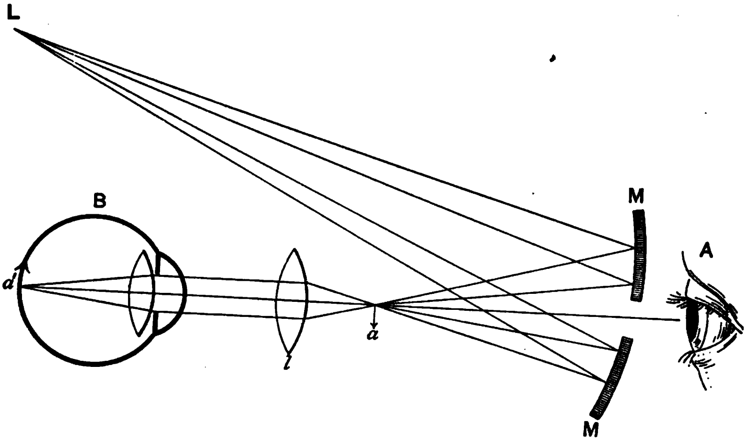

Fig. 159. Diagram to illustrate the Principles of a simple Form of Ophthalmoscope.

This method of using the ophthalmoscope is known as the "indirect" method. The retina may also be observed by the "direct" method, in which the reflecting mirror is placed immediately in front of the observed eye. An erect image of the retina is then seen (supposing the refraction of the observed eye is normal) which is larger than by the indirect method.

§ **776.** As to the meaning of the difference between rods and cones, we have no knowledge except in so far as visual purple is concerned. If the view mentioned in § 773 is correct, the rods are probably structures which chiefly have to do with vision at low intensities. Since it is in the fovea centralis that we have the most acute vision of both form and colour, the cones must be able to serve as the instruments of all visual sensations. The coloured globules intercalated between the outer and inner limbs of cones in some of the lower animals, such as birds and reptiles, have probably no closer relation to colour vision than has the yellow pigment of our own macula lutea.

With regard to what goes on in the other layers of the retina our ignorance is complete. We may fairly suppose that the events which take place in the inner limbs of the rods and cones are different from those which take place in the optic fibres. We may conclude that the latter are of the nature of nervous impulses, though we may here repeat what we have already urged, namely, that it is hazardous to infer that the little we know of motor nervous impulses may be applied with little or no modification to sensory nervous impulses; but as to the nature of the events in the inner limbs of rod and cones, or as to what happens in the intervening layers of the retina, we know nothing.

§ 777. The little objective knowledge which we possess concerning retinal processes is almost limited to the detection of electric currents. The retina and optic nerve like other nervous structures develope electric currents which may be spoken of as currents of rest and currents of action. They may be shewn by placing one electrode on the retina of a bisected eye, or on the cornea of a whole one, and the other on the optic nerve, or hind part of the eyeball or on the cortical visual centre or even on some distant part of the body. They are also manifested by the isolated retina itself. The phenomena appear somewhat complicated by the appearance now of positive, now of negative variations; but this fact comes out clearly, that the incidence of light on the irritable retina develops an electric change, the magnitude of which is to a certain extent proportionate to the intensity of the light acting as a stimulus. The changes gradually diminish and disappear as the retina gradually loses its irritability. We may add that these electric phenomena appear to be quite independent of the condition of the visual purple.

## SEC. 10. ON SOME FEATURES OF VISUAL SENSATIONS ESPECIALLY IN RELATION TO VISUAL PERCEPTIONS.

§ **778.** In our previous study of visual sensations we dealt chiefly with the more simple and fundamental characters of sensations; we considered each sensation by itself and discussed its features irrespective of the influence of other sensations excited at the same time, except so far as it became necessary, in treating of the localisation of sensations, to speak of the circumstances which determined the fusing of two neighbouring sensations into one. It very rarely occurs however that any object or event in the external world gives rise to a simple sensation such as those on which we have dwelt; each part of the external world, each external object such as a tree, is the source of many distinct sensations differing from each other in intensity and other characters. In looking at a tree we are conscious of many sensations of different colours and intensities, each having a definite localisation; but these are coordinated in our consciousness into a whole and we say we "see a tree." The effect which the whole visible world has upon us is not that of a multitude of single sensations each separate from and independent of the other, but of a smaller though still large number of groups of sensations corresponding to what we call the objects of nature. And we have now to turn our attention to certain facts concerning vision which become especially prominent when we are the subject not of an isolated single visual sensation but of complex groups of simultaneous visual sensations. The sum of visual sensations and groups of sensations which are excited by images falling on the retina at any one time, we call, as we have already said (§ 666), the 'field of vision,' or 'visual field.'

§ **779.** Before we proceed any further however it will be well to call to mind that in studying vision as we are now doing by means of an appeal to our own consciousness, we are deserting the ordinary methods of physiology for the methods which are more strictly speaking those of psychology. Or rather in our study of vision we are using both methods, suddenly turning from one to the other. We are using ordinary physiological methods when we are studying how the various rays of light proceeding from a tree form an image of the tree on the retina, and how these rays thus falling on the retina give rise to visual impulses. But when we study the change in our consciousness which is brought about by the visual impulses thus excited through the image of the tree falling on the retina, we are dealing with psychological problems. The object, the tree itself, and our vision of it, the one being commonly spoken of as the cause of the other, are connected by a chain of events; one end of the chain we study by physiological, the other end by psychological methods; and the difficulty of our task arises from the fact that we have to use these two different methods for a common purpose, namely that of explaining how the tree gives rise to the vision of it.

When we turn to the physiological side of the problem we cannot at present say much more than that the rays of light proceeding from the tree give rise to the changes in the optic fibres which we have called visual impulses. We have seen in dealing with the brain reason to think (§ 643) that visual impulses, like other sensory impulses, may influence the working of the central nervous system without producing any such change of consciousness as can be studied by psychological methods; and we further suggested (§ 673) that in the structures of the mid-brain which we called the primary visual centres a visual impulse underwent a development by which it became no longer a mere impulse but something more, and that the changes in these primary visual centres transmitted to the occipital cortex gave rise there to the changes with which the distinct affection of consciousness is associated. It is undesirable to speak of the events in the primary visual centres as "sensations," since it is convenient to reserve this term for the psychical events, the changes of consciousness of which we can become aware by examining our own minds; nor is there at present any need to give them any name at all; but it is important when we are using the psychological method to remember that between the physiological visual impulses and the psychological sensation there are events which must not be ignored.

Turning now to the psychological side of the problem we find that the psychical events are also complex, and that the psychical effects due to the same visual impulses are not all of the same kind. This is seen even in the case of simple and isolated visual sensations. Taking the effect of a luminous point, shining for a moment only, as a simple form of visual sensation, we must distinguish what we may call the mere change of consciousness, the mere sensation of light, from the further psychical effect of which we have already spoken and through which we associate the sensation with a luminous point occupying a particular position in external nature. Though the latter always accompanies the former, though whenever we experience a visual sensation we refer it to its cause in the external world, we can dissociate the two in our minds, and can speak of the mere sensation independently of the further psychical action. When we have vision not of such a simple object as a luminous point, which we may consider as giving rise to a single sensation, but of a tree which gives rise to a complex group of sensations, the psychical actions which accompany the mere sensations are manifold and become prominent in the total visual effect produced by the tree. That total visual effect is determined not only by the sensations to which the retinal image of the tree is at the time giving rise, but also by various psychical events dependent on the previous knowledge of the nature of trees which we have gained by touch as well as by sight, and on other circumstances. In common language we distinguish between the mere sensation and the further psychical visual effect by saying that we 'feel' a sensation and 'perceive' an object; and, though the term 'perception' has been employed in different meanings by different writers, we may here make use of it, in what is perhaps its most usually accepted meaning, to denote the further visual effect to which we have just called attention as distinguished from the immediate sensation. We feel a sensation of light, and we may feel at one and the same time a number of such sensations of different intensity and quality; we perceive an object, it may be a simple object such as a mere transient flash of light or a complex object such as a tree or a scene.

From what we have said above it follows that, although it is perfectly true as we have insisted (§ 702), that our perception of external objects is based on the optical sharpness of the retinal image, and on the distinctness of the several sensations which the retinal image excites, we should be wrong in supposing that when an image of an object is formed on the retina the visual impulses correspond exactly to the retinal image, the sensations correspond exactly to the impulses, and the perception corresponds exactly to the sensations, so that the perception is as it were a "mental image" corresponding exactly to the retinal image and hence to the object itself. The truth lies in the contrary direction; things are not what they look, or, since the same applies to other senses besides vision, what they seem; and one object of philosophy is to ascertain the exact relations between things as they are and things as we think them to be. We must of course confine ourselves here to pointing out, in regard to vision, some of the more salient differences which obtain between the actual features of an object and our perception of the object.

Of these differences some are clearly of psychical origin. Our perception of a tree is in part determined by events other than the actual sensations, by psychical processes arising out of our previous experiences of trees, and in other ways. Some of these psychical processes we shall consider a little later on.

Other differences are either clearly or possibly of physiological origin; the view may at least be argued that they arise either during the retinal changes through which visual impulses are developed or during the subsequent cerebral changes, spoken of above, through which the visual impulses give rise to visual sensations; and it is to some of these that we wish first to call attention.

§ **780**. *Irradiation.* A white patch on a dark ground appears larger, and a dark patch on a white ground smaller, than it really is. In Fig. 160, the white square on the right-hand side looks larger than the black square on the left-hand side though both are exactly of the same size. So also neighbouring white surfaces tend to melt together. The effect is increased when the object is somewhat out of focus, and may be then partly explained by the diffusion circles which, in each case, encroach from the white upon the dark. But over and beyond this, any sensation coming from a given retinal area occupies a larger share of the field of vision when the rest of the retina and central visual apparatus are at rest, than when they are simultaneously excited. It is as if the neighbouring, either retinal or cerebral, structures were sympathetically thrown into action at the same time. In this way a certain difference is established between the retinal image and the perception.

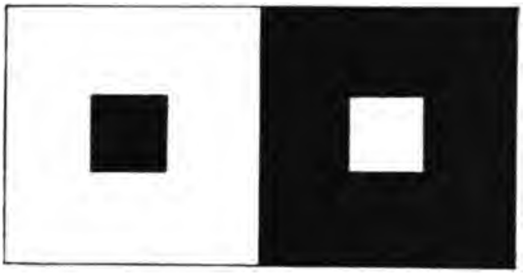

FIG. 160.

§ **781.** *Simultaneous contrast.* If a white strip be placed between two black strips, the edges of the white strip, near to the black, will appear whiter than its median portion; and if a white cross be placed on a black background, the parts close to the black will appear sometimes so white, compared with the centre of the cross, that the latter will seem dim or even shaded. This effect, which occurs even when the object is well in focus, is spoken of as one of 'simultaneous contrast'; the increased sensation of light which causes the apparent greater whiteness of the borders of the cross is regarded as the result of the 'contrast' with the black placed immediately close to it. Still more striking results are seen with coloured objects. If a book, or pencil, be placed vertically on a sheet of white paper, and illuminated on one side by the sun, and on the other by a candle, two shadows will be produced, one from the sun which will be illuminated by the yellowish light of the candle, and the other from the candle which will in turn be illuminated by the white light of the sun. The former naturally appears yellow; the latter, however, appears not white but blue; it assumes, by contrast, a colour complementary to that of the candle-light which surrounds it. If the candle be removed, or its light shut off by a screen, the blue tint disappears, but returns when the candle is again allowed to produce its shadow. If, before the candle is brought back, vision be directed through a narrow blackened tube at some part falling entirely within the area of what will be the candle's shadow, the area, which in the absence of the candle appears white, will continue to appear white when the candle is made to cast its shadow, and it is not until the direction of the tube is changed so as to cover part of the ground outside the shadow, as well as part of the shadow, that the latter assumes its blue tint. If a small piece of grey paper be placed on a sheet of pale green paper, and both covered with a sheet of thin tissue-paper, the grey paper will appear of a pink colour, the complementary of the green. This effect of contrast is far less striking, or even wholly absent, when the small piece of paper is white instead of grey, and generally disappears when the thin covering of tissue-paper is removed. It also vanishes if a bold, broad, black line be drawn round the small piece of paper, so as to isolate it from the ground colour. And many other instances of this kind of contrast might be given. It is obvious that whenever in vision this effect intervenes, a discrepancy is introduced between the features of an object and our perception of them. But before we attempt to point out the exact manner in which the effect is produced, it will be convenient to turn to some other effects which are also sometimes spoken of as those of "contrast."

§ **782.** *After-images. Successive contrast.* As we have already (§ 748) seen the visual sensation lasts much longer than the stimulus, and under certain circumstances the sensation is so prolonged that it is spoken of as an after-image. Such after-images are best developed when an eye, which has for some time been removed from the influence of light, is momentarily exposed to a somewhat strong stimulus. Thus if immediately on waking from sleep in the morning the eye be directed to a window for an instant and then closed, an image of the window with its bright panes and darker sashes, the various parts being of the same colour as the object, will remain for an appreciable time.

When, however, the eye has been for some time subjected to a stimulus, the sensation which follows the withdrawal of the stimulus is of a different kind; the result is what is called a *negative after-image*, or *negative image*, to distinguish it from a *positive after-image*, like the one mentioned above, which is simply a continuation of the sensation primarily excited with all its characters unchanged except that of intensity. If, after looking stedfastly at a white patch on a black ground, the eye be turned to a white ground, a grey patch is seen for some little time. A black patch on a white ground similarly gives rise when the eye is subsequently turned towards a grey ground to a negative image in the form of a white patch. This may be explained as the result of exhaustion. When the white patch has been looked at steadily for some time, that part of the retina on which the image of the patch fell has become tired; hence the white light, coming from the white ground subsequently looked at, which falls on this part of the retina, does not produce so much sensation as in other parts of the retina; and the image, consequently, appears grey. And so in the other instance; in this case, the whole of the retina is tired, except at the patch; here the retina is for a while most sensitive, and hence the white negative image. In speaking of the retina being tired we are using these words for simplicity's sake. We have no right to suppose that the exhaustion takes place in the retinal structures only; it may occur in the central cerebral structures during the development of visual impulses into sensations; indeed the chief part of it is probably of such a cerebral origin.

When a red patch is looked at, and the eye subsequently turned to a white or to a grey ground, the negative image is a greenish blue; that is to say, the colour of the negative image is complementary to that of the object. Thus also orange produces a blue, green a pink, yellow an indigo-blue, negative image, and so on; the negative image is in each case complementary to the primary one.

Similarly, when the eye, after looking at a coloured patch, is turned, not to a white or grey but to a coloured ground, the colour of the negative image is a mixture of the colour complementary to the primary image with the colour of the ground; if a yellow ground be chosen after looking at a green object, the negative image will appear as a mixture of red and yellow, a reddish yellow; and so on.

Though these negative images only become striking after a prolonged or intense excitation of the retina, such as rarely occurs in ordinary vision, still the effect must intervene, even if to a slight extent only, in our daily sight, and proportionately contribute to the discrepancy between the perception and the object.

Intervening between the original excitation and the after-image is another phenomenon, which is known as the "recurrent" image. This image follows the original sensation at a very short interval (about one-fifth of a second, or less) and is most easily observed when the stimulus is moving. A patch of light moving at a suitable rate is seen to be followed by a fainter patch. This recurrent image is colourless or only faintly coloured whatever the original colour of the stimulus. It is brightest with green light, and does not occur with red light. The interval at which it follows the original is lessened, and its brightness increased in dark-adaptation of the eye. These facts have been held to shew that the recurrent image depends on the stimulation of visual purple, which is supposed to be more inert than the other retinal substances.

§ **783**. The phenomena of 'simultaneous' and 'successive contrast' are further of interest in relation to the theory of colour vision; and we may venture for a little while to consider them in this connection. The mere occurrence of the negative images can be explained as a result of exhaustion on either hypothesis of colour vision. According to the Young-Helmholtz theory when the coloured patch is looked at, one of the three primary colour sensations is much exhausted, and the other two less so, in varying proportions, according to the exact nature of the colour of the patch; and the less exhausted sensations become prominent in the after-image. Thus, the red patch exhausts the red primary sensation, and the negative image is made up chiefly of green and blue sensations, that is, appears to be greenish-blue, or bluish-green, according to the particular hue or tone of the red. So also the yellow patch exhausts both the red and green sensations, leaving the blue only to make itself felt. On Hering's hypothesis, we may suppose that, owing to the continued effect of looking at the red patch, the katabolic changes of the red-green substance become less and less, leading to a prominence and indeed to an actual increase of anabolic changes in the same substance; hence, the sensation of green dominating in the negative image; and we may suppose that like events occur in the yellow-blue substance.

So far the facts suit both theories, but Hering's theory offers a more ready explanation than does the rival theory of the fact that it is easier to produce a negative green image after positive exposure to red, or negative blue after positive yellow than, *vice versâ*, red after green, or yellow after blue; in other words, that the red and yellow sensations are more readily exhausted than the green and blue sensations, as indeed is shewn by general experience. For all living substances are more prone to katabolic than to anabolic changes, destruction is easier than construction. Further, several phenomena of colour vision, to some of which we have already alluded, seem explicable on the view that the stock so to speak of red-green substance in the retina is sooner exhausted than the stock of yellow-blue substance, and this in turn than the white-black substance.

The Young-Helmholtz theory does not explain so readily as does the other why negative images often follow upon positive images without any stimulation of the retina subsequent to the primary one. As we have already said, if a white patch on a black ground be looked at for some time, and the eyes be then shut, a negative image of the spot will be seen on the ground of the 'intrinsic light' of the retina much blacker than the ground, and having in its immediate neighbourhood a sort of bright corona. Conversely a black patch on a white ground will give rise to a patch of exaggerated 'intrinsic light' in contrast to the blackness of the rest of the field. So also, if a window be looked at and the eyes then closed, the positive after-image with bright panes and dark sashes gives way to a negative after-image with bright sashes and dark panes. On Hering's theory all this is readily intelligible as a mere physiological process. On this theory the retina, or rather the visual apparatus, has to return to equilibrium after every exposure to light of any kind; the part of the retina giving rise to the sensation of black, whether it be the patch or the general ground, is not in a condition of equilibrium at the moment of shutting the eyes, the white-black substance is here undergoing anabolism in excess; and, when the light is wholly removed, it passes into equilibrium by katabolic changes, and in doing so developes a sensation, a feeble sensation it may be but still a sensation, of white. The Young-Helmholtz theory cannot offer any such physiological explanation; black being the effect of the absence of all stimulation from the visual apparatus cannot be followed by any physiological rebound; and the theory has to seek a psychological explanation. The parts of the visual apparatus which had been stimulated by light, give rise when the eyes are shut to a sensation of black, and the parts which had not been stimulated, appear in contrast with these to yield a sensation of light; but only appear, the effect is a psychological, not a physiological one.

Hering's theory also offers a physiological explanation of the fact that not only in the case of black and white, but also in the case of colours, the negative after-image with its black, green, &c., corresponding to the white, red, &c., of the positive image, may give way to a return of the positive image with all its original features, to be succeeded by a second negative image like the first, and thus often by a whole series of alternate positive and negative images, each gradually becoming fainter and more obscure. For such rhythmic oscillations from one sensation to its complementary or correlative and back again, pointing to katabolism and anabolism alternately gaining the upper hand, are not without analogies in other common instances of the metabolism of living substance. We may of course apply a like hypothesis to the three primary sensations, but the explanation of the phenomena, as thus given, is not so direct as that afforded by Hering's theory, especially when we consider that each occurrence of the negative image of black has to be accounted for on psychological grounds.

On somewhat the same line of argument, the phenomena of simultaneous contrast may be appealed to in favour of Hering's theory. The explanation of these effects, given by the supporters of the Young-Helmholtz theory is, like that offered for the negative image of black, a psychological one. In the case for instance of the grey patch seen as pink in the midst of a green field, it is argued that the patch does not actually excite a sensation of pink but that we think it is pink because we attribute the greenness of the whole field to the covering tissue paper, and seeing the patch shine through this judge the patch to be reflecting just those rays, namely pink, which mixing with the green would give rise to white, that is to a colourless grey. And a similar psychological explanation has been given of the other cases of simultaneous contrast. Such an explanation is in itself not very convincing; and against it may be urged the fact that in the cases quoted the predominance of the primary colour over the field is not necessary for the effect; and yet the interpretation is based on this. Moreover an experiment may be so arranged that a marked effect of simultaneous contrast should present itself in the vision of one eye but not of the other; now we can hardly imagine that, when both eyes are being used, we can interpret in different ways the sensations derived through the two eyes.

Conclusive evidence that contrast is mainly dependent on physiological processes is afforded by the fact that contrast effect will influence the point of fusion with intermittent stimulation of the retina. As we have seen in § 749, the rate at which successive stimuli must follow one another in order to fuse into a continuous sensation varies with the difference of brightness between the stimuli, and it has been found that this point of fusion is very much influenced when the successive stimuli are so arranged as in

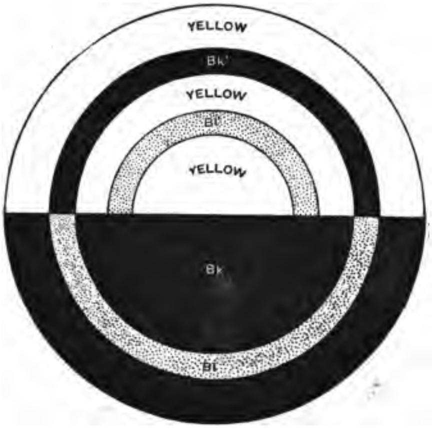

**Fig. 161.** (Sherrington.)

the disc shewn in Fig. 161, that the one is increased in brightness, the other diminished in brightness by the effect of contrast. This disc shews two rings, each half blue and half black. In the outer ring, the blue half, *Bl*, is increased in brightness by contrast with the surrounding black, and the black half, *Bk'*, is intensified, rendered more black, by contrast with the surrounding yellow. In the inner ring, on the other hand, the blue half, *Bl'*, is darkened by the surrounding yellow, and tends to approach the black half of the ring, *Bk*, in luminosity. On rotation on the colour top, the outer ring shews highly marked flicker when complete fusion has taken place in the inner ring, and a much higher rate of rotation is necessary to abolish flicker in the outer than in the inner ring. In this experiment two rings, in each of which the physical stimuli are exactly the same, shew a marked difference in behaviour owing to the influence of contrast.

Hering's theory offers a direct physiological explanation of contrast; it supposes that when one part of the retina is stimulated, the neighbouring portions of the field of vision are affected at the same time in a manner which may be roughly but only roughly compared to electric induction, so that they undergo changes antagonistic or complementary to those going on in the part of the field of vision corresponding to the portion of the retina actually stimulated. Thus in the case of the grey patch on the green field, the anabolism of the red-green substance in the green field surrounding the grey patch leads to a certain amount of katabolic action of the red-green substance within the grey patch, and so gives rise to a red sensation. In a similar way the bright corona seen round the black negative image developed by shutting the eyes after staring at a white patch on a black ground is due to the anabolism in the black negative image inducing katabolism of white-black substance, that is a sensation of (white) light, in its immediate surroundings. It will of course be understood that the theory does not maintain that the effect is necessarily produced in the retina itself; it may be developed in the visual centres, or in them and in the retina together. We must not go into further details, but we may add that many of the details of these effects of simultaneous contrast are more easily explained on Hering's theory when the possibility of such an inductive action is admitted than by any psychological hypothesis.

We have, contrary to our wont, dwelt so long on two contending theories, and have here renewed our discussion of them in connection with their effects of contrast, partly because of the intrinsic interest of the matter, but also, and not least, because an attempt to decide between the two views opens up important lines of thought and leads to considerations which must have great influence on our conceptions not only of visual sensations but also of all sensations, and indeed of nervous processes in general. We have not attempted anything like a full discussion of the subject; we have only ventured to indicate some of the leading criticisms which may be made on each theory; and so far as we are aware no crucial test between the two has as yet been brought forward. We may now leave the matter with the remark that while the Young-Helmholtz theory tends to lead us direct from the retinal image to the psychological questioning of the sensations, and seems to offer no bridge between the first step and the last, Hering's theory is distinctly a physiological theory, and at least holds out for us the promise of being able to push the physiological explanation nearer and nearer home before we are obliged to take refuge in the methods of psychology.

§ **784.** We have seen (§ 750) that visual sensations may be produced in other ways than by light falling on the retina. In such cases the effect which is produced upon our consciousness is wholly misleading. A mechanical or electrical stimulation of the retina may give rise to a visual sensation identical with that which would be produced by the rays from a flash of light falling upon a part of the retina. In both cases we should have a perception of a flash of light occurring in a certain part of the field of vision; and so far as the perception itself is concerned we could not distinguish between the latter which is a real and the former which is a false perception.

Not only single and simple sensations, but also complex groups of sensations may be excited by other means than that of light falling on the retina, and we may thus experience varied and intricate perceptions which have no objective reality at all. Many people when they close their eyes at night, or indeed at other times, see images of faces or other objects; and though under such circumstances it is easy to recognize the subjective origin of the perception, that conclusion is reached by reasoning upon the circumstances, and not because the perception itself differs in character from a like perception caused by looking at an external object. In such cases it is probable that some causes or other of a physiological nature give rise either in the lower visual centres or in the cerebral cortex to just such changes as would be induced by corresponding visual impulses, though those impulses are wholly wanting; in other words, the causes in question give rise to visual sensations, in the physiological meaning of that word, which produce a psychological effect identical with that of visual sensations produced in the ordinary way through the action of light on the retina. In some cases perhaps the process may begin even in the retina itself; abnormal changes in one or other of the retinal structures may lead to the development of complex coordinate visual impulses.

Sometimes the sensations and perceptions thus occurring, especially those which are met with on closing the eyes at night, may be recognized as revivals, more or less altered, of sensations experienced during the day; something sets going again the series of cerebral events which were set going by actual rays of light. At other times, there is no history of any like sensation having been felt in the immediate past; the psychical effect appears to have no objective cause at all. Moreover such false sensations and perceptions having a distinctness which gives them an apparent objective reality quite as striking as that of ordinary visual perceptions, may occasionally be experienced not only when the eyes are closed, but even when the eyes are open, and when therefore ordinary visual perceptions are being generated, with which they mingle and with which they are often confused. They are then spoken of as *ocular phantoms* or *hallucinations*. They sometimes become so frequent and obtrusive as to be distressing, and form an important element in some kinds of delirium, such as delirium tremens.

It is probable, as we have just suggested, that these false perceptions may be started by events, which in ordinary language may be called physiological; but the whole chain of events between the visual impulse, or even the immediate effect of the impulse which we may consider as the physiological sensation, and the terminal psychological perception is long and complex; the discordance between the perception and its apparent cause, in other words, the falsity of the perception, may be introduced in the later, psychological, links of the chain. And an hallucination may have such an origin that it may fitly be spoken of as purely psychological.

This naturally leads to the remark that a perception may be revived in the mind, without the usual physiological antecedents, as the result of purely psychological processes; it is then generally spoken of as an 'idea.' And we find, upon examination, that each new perception which we experience is more or less modified by memories and ideas resulting from bygone perceptions of a like kind. But we have already determined to defer the consideration of these and other more or less distinctly psychical modifications of perceptions until we have studied certain results arising from the use of two eyes.

## SEC. 11. BINOCULAR VISION.

§ **785.** So far we have treated of vision as if it were carried out by means of one eye and have only incidentally referred to our possessing two eyes. Our ordinary vision is, however, carried out by means of two eyes, our vision is binocular not monocular; and to the characters of this binocular vision we must now turn. In dealing with monocular vision we rarely had occasion to refer specially to the movements of the eyeball; but in binocular vision these play an important part; and even before we go into details, it will be desirable to point out not only certain general facts, but also the meaning of certain terms which we shall have to use.

The eye is virtually a ball placed in a socket, the bulb or eyeball and the orbit forming a ball-and-socket joint. In its socket joint the eyeball is capable of various movements, but these are limited to those of rotation within the socket; the eyeball cannot by any voluntary effort be moved out of its socket. It is stated that by a very forcible opening of the eyelids the eyeball may be slightly protruded; but this trifling locomotion may be neglected. By disease, however, the position of the eyeball in the socket may be materially changed.

The movements of rotation to which the eyeball is thus limited are carried out round a centre in the eye which is termed the *centre of rotation*, and which has been determined to lie in the vitreous humour about 13·5 mm. behind the anterior surface of the cornea, not quite 2 mm. behind what may be considered as the geometric centre of the eyeball; it is of course quite different from the optical centre or nodal point of the diagrammatic eye (§ 705).

When we direct our vision to a point, a line drawn from such a point, which we may call *the fixation point* of vision, to the centre of rotation, is called the *line of fixation*. From this must be distinguished the *visual axis* or *line of vision*, which is a line drawn from the fixation point through the nodal point to the centre of the fovea centralis. In most individuals the optic axis, the line on which the dioptric surfaces of the eye are centred, meets the retina on one side of the fovea (§ 704); hence in these the visual axis does not coincide with, and is different from the optic axis. When with both eyes we look straightforwards to the far distance, the visual axes of the two eyes are parallel; when we direct the two eyes to the same fixed point, the two visual axes converge to the fixed point, the amount of convergence being the greater the nearer the fixed point to the observer.

The horizontal plane in which the two visual axes lie is called the *visual plane*; and a vertical plane at right angles to this, midway between the two eyes, or more exactly bisecting a line, sometimes called the "base line" or "fundamental line" joining the nodal points of the two eyes, is called the *median plane*.

§ **786**. As we have seen, the sum of the sensations which we can receive from the retina at the same time is spoken of as the "visual field," or "field of vision." The term therefore has properly a subjective meaning, but it is sometimes used in an objective sense to denote the space or area of the external world, rays of light from which are capable of exciting the retina at any one time; where we wish to distinguish between the two, we may call the latter the "field of sight." The dimensions of the field of sight for one eye will even in the same individual vary with the width of the pupil and other dioptric arrangements of the eye; individual variations are also considerable; but the ordinary dimensions may be stated as subtending an angle of about 145° in the horizontal and about 100° in the vertical meridian, the former being distinctly greater than the latter. When an external object lies outside the area subtending these angles we say that it is outside the field of sight for that position of the eye; it may of course be brought into the field of sight by moving it or by moving the eye. The

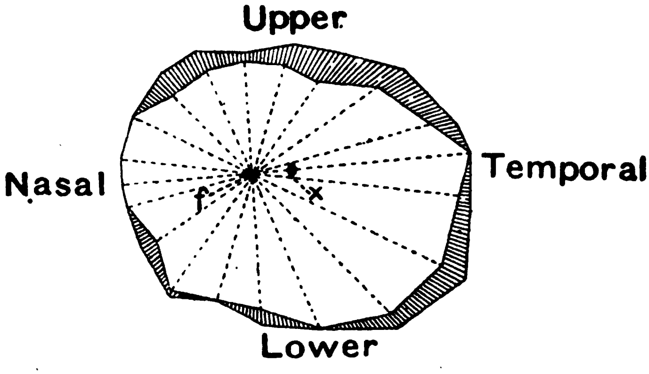

FIG. 162. THE VISUAL FIELD OF THE RIGHT EYE. (Aubert.)

The figure represents the visual field projected into space and therefore corresponds to the objective field of sight; the temporal side of the figure corresponds to the nasal side of the retina. The shaded part indicates the increase gained by looking outwards towards the temporal side. *f*, fovea; *x*, blind spot.

outline of the field is an irregular one, and stretches farther towards the temporal side of the fixed point, that is, towards the nasal side of the retina, than on the other side; it is somewhat larger and of a different form when the eye is turned towards the temporal side than when the eye is directed straight forwards; cf. Fig. 162. It will be understood that the two visual fields of the two eyes are unlike; cf. Fig. 163.

When we use both eyes a large part of the visual field of each eye overlaps that of the other; that is to say, the rays of light proceeding from a large part of the field of sight of each eye fall upon and affect both retinas. But at the same time a certain part of each visual field does not so overlap any part of the other. If the right hand be held up above the right shoulder and brought a little forward it soon becomes distinctly visible to the right eye, it enters into the field of sight of the right eye. But if the right eye be closed, the right hand kept in the former position is not visible to the left eye; it is outside the field of sight of that eye; it has to be brought much further forward until it comes into the field of sight of the left eye; the profile of the face and especially of the nose prevent the rays reflected from the hand gaining access to the left retina until the hand is brought a certain distance forward. The right-hand side of the objective field of sight of the right eye, corresponding to the nasal side of the retina of that eye, extends much farther to the right than does the right-hand side of the field of sight of the left eye, which corresponds to the temporal side of the retina of that eye; cf. Fig. 163. Similarly, the left-hand side of the field of sight of the left eye extends farther to the left than does that

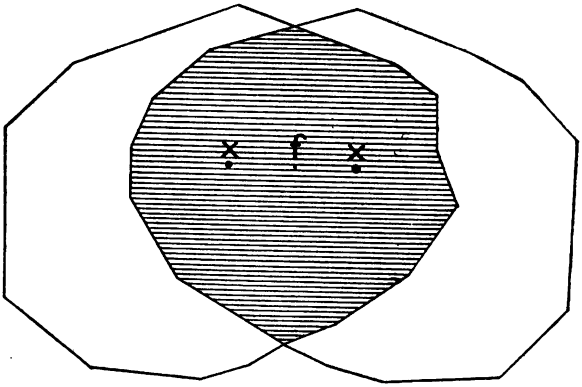

Fig. 163. The visual fields (fields of sight) of the two eyes when the eyes converge to the same fixed point. (Aubert.)

The shaded part is that common to the two eyes. *f*, the fixed point, corresponding to the fovea of each eye; *x*, the blind spots of the two eyes.

of the right eye. Hence on the one hand the total field of sight of the two eyes together is increased in the horizontal diameter, subtending on an average an angle of 180° instead of 145°; and on the other hand while a certain right-hand and left-hand part of the united fields of sight belong respectively to the right and left eye only, the remainder of the field is common to the two eyes. The area common to the two eyes when the visual axes converge to the same fixed point is shewn as the shaded part in Fig. 163. Rays of light from objects in the common part affect the retinas of both eyes at the same time, vision is here binocular; rays of light from objects at the extreme right and left affect only the right and left retina respectively, vision in these parts of each eye is never binocular, always monocular. The amount of each retina which is thus cut off from binocular vision is determined by the prominence of the nose and profile between the eyes; in some of the lower animals the position of the eyes is so completely lateral that no rays of light proceeding from the same object can fall on any part of the two retinas at the same time, and in these creatures vision is wholly monocular.

§ **787.** *Corresponding or Identical Points.* Though when we use two eyes, we must receive from every object in the field of sight common to the two eyes two sets of visual impulses, indeed we may say two sets of sensations, our perception of the object is under ordinary circumstances a single one; we see one object, not two. By putting either eye into an unusual position, as by squinting, we can render the perception double; we see two objects where one only exists. This shews that certain parts of each retina are so related to each other that when an image of an object falls on these parts at the same time, the two sets of sensations excited in the two parts are blended into one; such parts are spoken of as *corresponding* parts; they have also been called *identical* parts. Since in the ordinary movements of the eyes we see objects single, and do not receive double impressions unless we move the eyes in an unusual manner, it is obvious that the movements of the eyeballs and these corresponding parts of the two retinas are so related, the one to the other, that the former bring the images of objects to fall on the latter.

We can easily determine which are the corresponding parts of the two retinas by tracing out the paths of the rays of light falling on the two retinas, § 706. As we have said, when we look at an object with one eye the visual axis of that eye is directed to the object, and when we use two eyes the visual axes of the two eyes converge at the object, the eyeballs moving accordingly. The corresponding points of the two retinas are those on which the two images of the object fall when the visual axes converge at the object. Thus in Fig. 164 if *vl* from $X$ to $x$ and $X$ to $x'$ be the two visual axes, $x$, $x'$ being the centres of the foveæ centrales of the two eyes, then, the object $XYZ$

being seen single, the point *Y* on the one retina will 'correspond' to or be 'identical' with the point *Y′* on the other, and the point *Z* in the one to the point *Z′* in the other.

When the whole area of the retina in each eye which we use for binocular vision is explored in this way we find, as follows geometrically from the paths of the rays of light, that the upper half of one retina corresponds to the upper half of the other, the lower half to the lower half, the right side to the right side, and the left side to the left side. But when we turn to the structure of the retina we find that the left or nasal side of the right eye, since it contains the entrance of the optic nerve, is comparable with, not the left, but the right or nasal side of the left eye, and in like manner the right or temporal side of the right

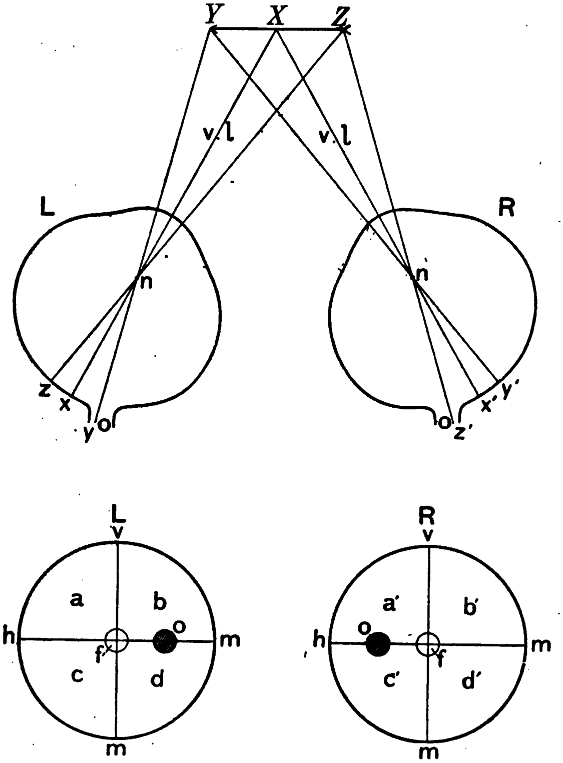

Fig. 164. Diagram illustrating corresponding points.

*L* the left, *R* the right eye, *n.* nodal point, *o.* optic nerve, *x.* fovea. *X′Y′Z′* are points in the right eye corresponding to the points *XYZ* in the left eye. *v. l.* visual axis. The two figures below are projections of *L* the left and *R* the right retina. *f.* fovea, *o.* blind spot. It will be seen that *a* and *c* on the *temporal* side of *L* corresponds to *a′* and *c′* on the *nasal* side of *R*. *v. m. h. m.* lines of separation.

eye is comparable with the left or temporal side of the left eye. Hence, considered in relation to the structure of the retina, the corresponding points appear to be reversed from side to side, though not from top to bottom. While the upper half of the retina of the left eye corresponds to the upper half of the retina of the right eye, and the lower to the lower, the nasal side of the left eye corresponds with the temporal side of the right, and the temporal of the left with the nasal side of the right.

It will be observed that in each eye a vertical plane through the visual axis (*v. l.* in Fig. 164) cuts the retina in a vertical line *v. m.*, which divides the retina into two lateral, temporal and nasal, halves, each temporal and each nasal half corresponding with the nasal and temporal half respectively of the other eye. When the visual axes of the two eyes are parallel, the two vertical planes in question are approximately parallel to the median plane and to each other. Further, a horizontal plane drawn through the visual axis at right angles to the above vertical plane cuts the retina in a horizontal line *h. m.*; and this also divides the retina into two halves, an upper and lower half, the upper and the lower halves of both retinas being corresponding. These two lines, each of which may be considered as a series of corresponding points, are sometimes spoken of as *lines of separation.*

Points which do not correspond to one another are often called "*disparate*" points. When disparate points are stimulated by an object, the object is (except as we shall see in certain cases) seen double. The nature of this double vision, or *diplopia* as it is called, will vary according as the object giving rise to the images is nearer or farther than the fixation point, the point on which the visual axes are converged. When an object is seen double and one eye is closed, the image really belonging to that eye will disappear, the retina of that eye cannot be affected by the object. But if the object seen double is nearer than the fixation point, the image which is lost will be that which is seen on the opposite side; if the right eye be closed, the left-hand image will disappear; in this case the "*diplopia*" is spoken of as "*crossed*" or "*heteronymous.*" If, on the other hand, the object seen double is beyond the fixation point, the diplopia is "*uncrossed*" or "*homononymous*"; closing one eye will make the image of the same side disappear.

Single vision occurs not only when corresponding points are stimulated, but also when disparate points are stimulated, provided that the departure from correspondence is slight. In the latter case, as we shall see later, the object seen receives a different localization to one stimulating corresponding points. It is obvious that in single vision with two eyes the ordinary movements of the eyeballs must be such as to bring the visual axes to converge at the object looked at. It is therefore important to study in some detail the movements of the eyeballs, by means of which, in ordinary vision, the relative positions of the two retinas are so carefully adjusted that we habitually see objects single, not double.

§ 788. *The Movements of the Eyeball.* As we have said, the movements of the eyeball are movements of rotation round an immobile centre, the centre of rotation; but these movements are limited in a particular way, and it is necessary to pay attention to their characters and limitation.

One position of the eyeball, for reasons which we shall see presently, is called the *primary position,* and it will be desirable to start from this position. Though its exact determination requires special precautions it may be described as that which is assumed when, with the head erect and vertical, we look straightforwards to the distant horizon; the visual axes of the two eyes are then parallel to each other and to the median plane.

Let us now suppose three axes drawn through the centre of rotation, in the three planes of space:—one, the visual axis itself, which we may call the longitudinal axis; another at right angles to this and horizontal, the horizontal axis; and a third also at right angles, but vertical, the vertical axis. Corresponding to these three axes we have three main possible movements of rotation. The eyeball might be rotated round the vertical axis so that the visual axis moved from side to side. It might be rotated round the horizontal axis so that the visual axis moved up and down. And lastly, it might be rotated round the longitudinal axis, the visual axis itself remaining motionless and the pupil turning round like a wheel.

Now we can easily carry out by an exercise of the will the first and second of these movements. We can easily move the eyes up and down, rotating them on the horizontal axis, as when we look up to the heavens or down to the ground. We can also move the eyes from side to side, rotating them round the vertical axis, as when we look to the right or to the left. We can move the two eyes sideways together in the same direction keeping the visual axes parallel, or we may move them laterally in opposite directions, as when the visual axes being parallel we make them converge, or when convergent bring them back to or towards parallelism. And we can combine rotation round the horizontal axis with rotation round the vertical axis, and so give oblique movements to the eyeball. We can do all this by an exercise of the will, but we cannot by any voluntary effort carry out the third kind of movement, we cannot rotate the eyeball round the visual axis, we cannot twist the eye in a swivel movement round its longitudinal axis. There are certain movements of the eye in which such a swivel rotation, if we may so call it, does to a certain extent take place, and when we induce these movements we do bring about such a swivel rotation; but we cannot bring about swivel rotation by itself, we can only effect it as part of the particular movements in question.

And there is a reason why we are thus limited as to our power of moving the eyeball. In both rotation round the horizontal axis, and rotation round the vertical axis and in all the various combinations of these two movements which are possible, the two "lines of separation" (§ 787) on both the retinas keep their places; there is no dislocation of the corresponding regions of the two retinas. Obviously the two retinal circles in the lower part of Fig. 164 could be rotated round the vertical or round the horizontal axis or round any intermediate oblique axis without the two images of an external object ceasing to fall on corresponding parts. But if the retinal circles were twirled round their respective visual axes, the lines of separation, *v. m.* and *h. m.*, would rotate in a clock-hand fashion, and if the movements of the two eyes were unequal or in opposite directions, a dislocation of corresponding parts would ensue, and vision would become double. The limitation to the movements of the eyeball so as to avoid a swivel rotation is in the interests of binocular vision.

§ **789.** Not only do we find ourselves thus limited in our power when we attempt by a direct effort of our will to execute particular movements of the eyeball, but a similar limitation obtains in the natural movements of the eye in vision. The various movements of the eyeballs which we carry out when we are looking at things conform to a general law, which is known as "Listing's law," and which may be described as follows.

We stated a little while back that the "primary position" of the eyeball is one in which the visual axis lies parallel to the median plane and is directed to the distant horizon. When the eyeball is changed from this primary position into any other position, all of which may be called secondary positions, the change is effected without any swivel rotation round the visual axis itself; the visual axis may be directed up and down, or from side to side, or in any intermediate oblique manner without any such swivel rotation taking place. In other words, the movements by which the eyeball is brought from the primary position into any of the secondary positions are, in all cases, movements of rotation round the horizontal axis, or round the vertical axis, or round an axis, which though oblique, being neither horizontal nor vertical, lies in the same plane that they do; that is to say, every movement from the primary to a secondary position is a movement of rotation round an axis lying in a plane which passing through the centre of rotation is vertical to the visual axis.

The experimental proof of "Listing's law" may be obtained by the help of negative images (§ 782) in the following manner. Let the eye be directed to a grey wall or board which, otherwise of uniform appearance, is marked by parallel vertical and horizontal lines, placed at some little distance from each other so as to give a pattern of squares. At one of the intersections, which is to be used as the fixed point of vision, place two narrow strips of red paper in the form of a cross, one vertical, coinciding with the vertical line, and the other horizontal, coinciding with the horizontal line. Having brought the eye carefully into the primary position stare at the red cross until on turning the eye away a green negative image is produced. If now the vision be directed from the fixed point either up or down along the vertical line of the pattern on the wall, or from side to side along the horizontal line, it will be found that the cross of the negative image coincides in turn with each of the crosses of the pattern on the wall, the horizontal limb coinciding with a horizontal line and the vertical limb with a vertical line. This shews that during the up and down and during the side to side movement, during the rotation of the eyeball round its horizontal or round its vertical axis, no swivel rotation has taken place, for otherwise the negative image would have been turned round, and its cross would make an angle with the image of the cross on the wall. If the pattern on the wall be changed so that the lines while still at right angles to each other are oblique, not vertical and horizontal (this is most conveniently done by using not a wall but a large board and turning the board round), and the observation be repeated except that the eye is turned not vertically or horizontally but obliquely so as to follow the lines of the pattern, it will still be found that the cross of the negative image coincides with the cross of the pattern, and that whatever be the angle round which the board has been turned. This shews that Listing's law holds good not only for up and down and side to side movements but also for oblique movements, for movements of rotation round an axis which whatever its obliquity lies in a plane at right angles to the visual axis.

The same result as regards oblique movements may be obtained in another way even while the lines of the wall or board are allowed to remain vertical or horizontal. If in this case the eye be directed not up and down, or from side to side, but diagonally from the fixed centre in the middle of the board to one of the corners of the board, the cross of the negative image will not coincide with the cross of the pattern at the corner but will appear to slant; it will appear to slant to the right in the right-hand upper and left-hand lower corner, to the left in the left-hand upper and right-hand lower corner. The slanting cannot be due to a swivel rotation, since in that case the slanting would be in the same direction at both right-hand corners, and would be contrary to that occurring at both the left-hand corners. The discrepancy between the cross of the negative image and the cross of the pattern at the corner is to be explained by the fact that a horizontal line in the extreme upper part or in the extreme lower part of the field of vision appears to us curved, bent up or down at each right or left end of the line; and a vertical line in the extreme lateral part of the field of vision appears also curved, bent to the right or left at each, upper or lower, end of the line. Hence in the experiment in question we are comparing the cross of the negative image, not with a rectangular cross in the pattern, but with one, the arms of which seem to dip one way or the other and the two crosses necessarily slant towards each other. Our mind, however, corrects this dip, and regards the cross of the pattern as still rectangular, and in so doing judges the obliquity to belong to the negative image. The experiment therefore really proves that the cross of the negative image undergoes no twisting while the eye is being directed from the centre of the board to the corner, though at first sight it seems, and once was thought, to prove the contrary.

In the ordinary movements of the eye, then, a swivel rotation round the visual axis does not take place; and this limitation, since it holds good for the two eyes used together, as well as for one eye used by itself, serves to secure single vision with two eyes inasmuch as it avoids changes which might cause the images of external objects to fall on the parts of the two retinas which were not "corresponding parts." In certain movements of the eyes, however, a certain amount of swivel rotation does take place. This is especially seen in somewhat unusual movements. For instance when the head is turned down to the shoulder, or again when in directing vision to any object the head is moved from side to side, the eyes only partially move with the head; they tend to remain stationary, very much as the needle of a ship's compass remains stationary when the head of the ship is turned. The change in the position of the visual axes to which the movement of the head would naturally give rise is partially met by compensating movements of the eyeballs; were it not so, steadiness of vision would be impossible; and these compensating movements are found, on careful examination, to include a certain amount of swivel rotation round the visual axes. In certain other more usual movements some amount of such a swivel rotation is also present; and indeed, though so long as the visual axes remain parallel, movement in any direction may take place without any such rotation, a slight amount does intervene during convergence of the visual axes, as when we turn our eyes from a distant to a near object. On careful examination, however, it appears that such an amount of swivel rotation as does take place is after all for the purpose of securing the end that corresponding parts of the two retinas should be affected by the same external object; and, though we cannot here enter more fully into the subject, we may say that not only the more general movements of the eye which obey Listing's law, but also those which form an exception to it, appear to be carried out in the interests of binocular vision. We may now turn to the study of the ocular muscles, by the carefully coordinated contractions of which the various movements, on which we have dwelt, are brought about.

§ **790**. *The muscles of the eyeball* or *ocular muscles.* The eyeball is moved by six muscles, four of which are straight, *musculi recti, inferior, superior, internus* and *externus*, and two oblique, *musculi obliqui, inferior* and *superior.* The four straight muscles, taking origin from the back of the orbit around the sphenoidal fissure and the entrance of the optic nerve, are directed, as their name indicates, straight forward (the superior rectus however having a peculiar bend) and are inserted in positions corresponding to their several names into the sclerotic, behind the cornea, the bundles of fibres of the tendons being interwoven with those of the sclerotic. The tendon of the internal rectus on the nasal side of the eyeball is the broadest of the four; that of the superior rectus on the upper surface being somewhat narrower, and those of the inferior rectus on the under surface and of the external rectus on the temporal side, still narrower (Fig. 165). The insertion of the superior rectus lies nearer to that of the external rectus than to that of the internal rectus; its position therefore is not exactly in the middle line of the eyeball, indeed for two-thirds of its width it lies in the upper lateral quadrant of the sclerotic ring. The insertions of the external and of the internal rectus are both midway between the summit and bottom of the eyeball. The insertion of the internal rectus is the one closest to, and that of the superior rectus the one farthest away from the cornea, and the latter slants so as to be nearer the cornea at its nasal than at its temporal end.

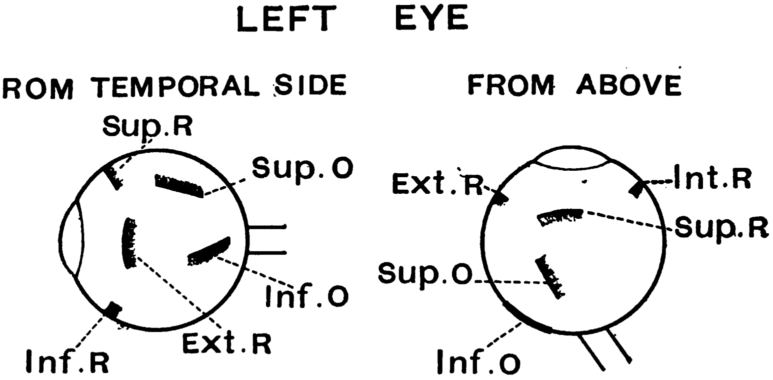

Fig. 165. The Left eye seen from A, the temporal side. B, from above, shewing the insertions of the Ocular Muscles. (Jessop.)

The superior oblique muscle, or trochlear or pathetic muscle, taking origin from the back of the orbit near the origin of the straight muscles and running forward internal to the superior rectus, ends in a tendon, which changing its direction by means of a pulley (*trochlea*), and passing beneath the superior rectus is inserted into the sclerotic in the upper region of the bulb towards its hind part. The line of insertion of the tendon (Fig. 165) runs obliquely from the temporal towards the nasal side, its mid-point lying not far from the vertical meridian of the eyeball.

The inferior oblique muscle arises from the front of the floor of the orbit on the nasal side; it is directed at first backwards to the temporal side, underneath the inferior rectus, between that and the floor of the orbit, and then passing upwards and backwards is inserted into the sclerotic underneath the external rectus in the hind temporal part of the ball. The line of insertion (Fig. 165) is also an oblique one like that of the superior oblique but it is placed somewhat farther past it; its hind end lies not far from the entrance of the optic nerve and it runs thence forwards and downwards.

§ **791.** The manner in which these muscles are thus severally attached to the eyeball suggests that in contracting they would move the eyeball in the following ways. Taking changes in the direction of the visual axis as indicating the nature of each movement we should expect that the superior rectus would turn the visual axis upwards, the inferior rectus downwards, the external rectus outwards towards the temporal side, and the internal rectus inwards towards the nasal side. The inferior oblique, its insertion being on the hind and lateral part of the eyeball, and the direction of the muscle being downwards, would in contracting turn the visual axis upwards, while the superior oblique having a somewhat similar insertion but acting in an opposite direction would turn the visual axis downwards. Both muscles however in thus raising or lowering the visual axis would, owing to the oblique direction of their insertions at the same time, turn it to the temporal side; the movement, as the names of the muscles suggest, would be an oblique one.

The six muscles therefore would seem to act as three pairs, the superior and inferior rectus, the internal and external rectus, and the inferior and superior oblique, each pair rotating the eyeball round a particular axis. Calculations based on a careful study of the attachments and directions of the several muscles, and the results of actual observations, shew that this is so, and that the movements carried out by the several pairs may be more accurately described as follows.

The superior rectus and the inferior rectus (see Fig. 166) rotate the eye round a horizontal axis, which may be described as one directed from the root of the nose to the temple; it is therefore not a line at right angles with the visual axis but one making an acute angle (20°) with such a line. The superior and inferior oblique rotate the eye round a horizontal axis which may be described as one directed from the centre of the eyeball to the occiput; it again is not a line at right angles to the visual axis, but makes an angle, with such a line, larger (60°) than the similar angle made by the inferior and superior rectus, and turned in a different direction. The internal rectus and external rectus rotate the eyeball round a vertical axis passing through the centre of rotation of the eyeball parallel to the median plane of the head when the head is vertical; this therefore is at right angles to the visual axis, and so differs from the other two.

When we compare the movements thus effected by these several pairs of muscles with the movements which we described above (§ 788) as the ordinary movements of the eye, namely movements of rotation round a vertical and round a horizontal axis both at right angles to the visual axis, we see that it is only the movements round the vertical axis which can be carried out by one pair of muscles acting alone, the particular pair being the internal and external rectus. Neither the horizontal axis of rotation of the inferior and the superior rectus, nor that of the oblique muscles, is placed exactly at right angles to the visual axis; each of them makes an oblique angle with that axis. Hence when in carrying out the ordinary movements of the eye we rotate the eyeball round the horizontal axis, we do not employ either of these pairs of muscles alone, but combine them, making use of one muscle of one pair with one of the other. The superior and inferior rectus in moving the visual axis up and down also turn

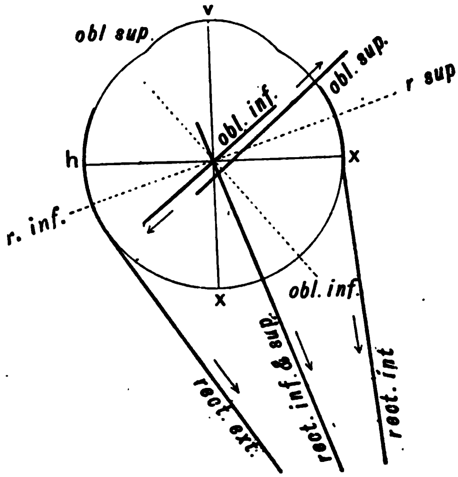

Fig. 166. Diagram to illustrate the actions of the muscles of the eye.

The eye represented is the left eye seen from above. The thick lines shew, by means of the arrows, the direction in which the several muscles pull, the beginning of each line also indicating the attachment of the muscle. The dotted lines indicate the axis of rotation of the superior and inferior rectus and of the oblique muscles. The axis of rotation of the internal and external rectus being perpendicular to the plane of the paper cannot be shewn. *v* x represents the visual axis and *h* x a line at right angles to it. (After Fick.)

it somewhat inwards, to the nasal side; but this is corrected if the oblique muscles act at the same time; and it is found that the rectus superior acting with the inferior oblique moves the visual axis directly upwards, and the rectus inferior acting with the superior oblique directly downwards in a vertical direction; that is to say, the two combinations rotate the eyeball round a horizontal axis at right angles to the visual axis.

Hence there are only two movements of the eyeball which we can carry out by the help of one muscle alone, namely that in which we simply turn the visual axis to the nasal side, employing the internal rectus, and that in which we turn it to the temporal side, employing the external rectus, the visual axis in both cases remaining in the same plane, the visual plane. In order to raise or lower the visual axis in the same vertical plane, without lateral movement, we must use two muscles; and if we wish to execute an oblique movement combining an up and down with a side to side movement of the visual axis we must employ three of the ocular muscles. These several movements, with the muscles concerned, may be stated as follows, the movement in each case being described with reference to changes in the direction of the visual axis.

| | | |
|---|---|---|
| Straight movements | To nasal side. | Internal rectus. |
| | To temporal side. | External rectus. |
| | Upwards. | Superior rectus and inferior oblique. |
| | Downwards. | Inferior rectus and superior oblique. |
| Oblique movements | Upwards and to nasal side. | Superior rectus, internal rectus and inferior oblique. |
| | Downwards and to nasal side. | Inferior rectus, internal rectus and superior oblique. |
| | Upwards and to temporal side. | Superior rectus, external rectus and inferior oblique. |
| | Downwards and to temporal side. | Inferior rectus, external rectus and superior oblique. |

The fact that in our ordinary movements of the eye we do thus combine the actions of muscles, and the advantages of such a combination are further shewn in connection with that swivel rotation of the eye round the visual axis itself, which, as we have seen, is wholly avoided in many of our movements and which we cannot carry out by a direct effort of the will. The superior rectus acting by itself, owing to the position of its insertion in reference to the direction of the fibres, not only turns the visual axis inwards while directing it upwards, but also to a slight extent rotates the eye round the visual axis; and the inferior rectus as well as both the oblique muscles in like manner tend in contracting to give the eyeball such a swivel rotation. This tendency of the superior rectus like its tendency to turn the visual axis inwards is counteracted by the inferior oblique, the swivel rotation of the latter being contrary in direction to that of the former; and the like tendency of the inferior rectus is in like manner counteracted by the superior oblique. Thus the movements, in carrying out which these muscles are combined, are rendered free from the swivel rotation element. On the other hand this tendency of the muscles in question is utilized in the particular movements in which the swivel rotation does take place.

§ **792.** *The co-ordination of the movements of the eyes.* The external rectus is governed by the sixth nerve, nervus abducens, the nucleus of which, as we have seen (§ 620), lies in the floor of the fourth ventricle in a position indicated by the eminentia teres. The superior oblique muscle is governed by the fourth nerve, nervus trochlearis, the nucleus of which (§ 622) lies in the floor of the aqueduct, in the region of the posterior corpus quadrigeminum. All the other ocular muscles are governed by the third nerve, the nucleus of which lies in the floor of the aqueduct in the region of the anterior corpus quadrigeminum; as we have said (§ 726), the fibres of the third nerve going to these ocular muscles seem to be more especially connected with the hind part of the nucleus.

From what has been said above it is obvious that, even in the movements of one eye, a coordination of the motor nervous impulses must in most cases take place. When we turn the visual axis outwards the motor impulses are confined to the sixth nerve, reaching the external rectus, and when we turn it inwards are confined to the third nerve, reaching the internal rectus; but in all other movements motor impulses must descend to at least two muscles along different nerve-branches, and in many cases must start from two or even all three of the cranial nuclei just mentioned. Even in movements of one eye there must be, in most cases, more or less coordination of actual motor impulses, in order to secure due efficiency of the movement; by actual motor impulses we mean impulses leading to the contraction of muscular fibres, irrespective of any influences which may at the same time be brought to bear on antagonistic muscles, in order to facilitate or qualify the movement.

But if this is true in the case of one eye, much more is it true when we use both eyes in binocular vision.

Two facts about binocular vision strike our attention. The one is that, as may be seen by watching the movements of any person's eyes, the two eyes move together. If the right eye moves to the right, so does also the left, and, if the object looked at be a distant one, exactly to the same extent; if the right eye looks up, the left eye looks up also; and so with regard to other movements. Very few persons are able by a direct effort of the will to move one eye independently of the other; though by some the power has been acquired. We shall refer immediately to particular movements in which one eye only is moved, while the other remains motionless. The other salient fact is that the movements of the two eyes are limited in certain ways. As we have seen, one of the simplest ocular movements is the side to side movement of the visual axis, and one of the commonest binocular movements is the convergence of the visual axes, as when we turn our eyes from something far off to something near, or conversely the change from considerable convergence to less convergence as when we turn our eyes from something near to something farther off. In a large number of instances this change to convergence from parallelism, or this increase or decrease of convergence takes place without any change in the visual plane, without any raising or lowering of the visual axes; in such instances the movement is carried out in convergence by the two internal rectus muscles, or in decrease of convergence by the two external rectus muscles; and the only coordination necessary is one which secures that the muscle of one eye should work in harmony with the muscle of the other eye. But even this relatively simple movement is limited in a very marked way. We can bring the visual axes of the two eyes from a condition of parallelism to one of almost any degree of convergence, but we cannot, without artificial assistance, bring them from a condition of parallelism to one of divergence. The stereoscope will enable us to create such a divergence. If in a stereoscope the distance between the pictures be increased very gradually so as carefully to maintain the impression of a single object, the visual axes may be brought to diverge; and the subject of the experiment may himself be made aware of the divergence, by the sudden removal of the instrument from his eyes; his vision of external objects is for a moment double, but for a moment only. This experiment shews the reason of the limitation of which we are speaking. So long as the visual axes are parallel or appropriately convergent the images of external objects fall on corresponding parts of the two retinas, and single vision results; when the visual axes are carried beyond parallelism, the images on the two retinas are not on corresponding parts and vision is double. Thus, as regards convergence or divergence of the visual axes, the movements of the two eyes are governed by the principle that the will can of itself only carry out those movements which are consistent with images of external objects falling on corresponding parts of the two retinas. There is an exception to this in the case of extreme convergence; we can as in squinting make the visual axes converge too much, and in consequence by a simple effort of the will can obtain double vision; but this is probably in order to leave a margin which shall secure our being able to use to the utmost our accommodation mechanism for near objects; otherwise the rule holds good. Not only so, but as the above experiment also shews, when we obtain divergence of the visual axes by artificial assistance, which is in itself directed towards securing single vision with the two eyes, the axes return, by an involuntary movement, to parallelism immediately that the assistance is done away with; the double vision occurring at the moment of removal of the instrument rapidly gives way to normal single vision. Other illustrations of the same principle may be met with. For instance, if a distant object be looked at with both eyes, but with a prism held horizontally before one eye, and if the image of the object be kept carefully single while the prism is turned very slowly from the horizontal to the vertical position, then on suddenly removing the prism a double image is for a moment seen; this shews that the eye before which the prism was placed had moved in disaccordance with the other. The double image, however, immediately after the removal of the prism, becomes single on account of the eyes coming into accordance.

When we examine all the various movements of the eyes which we are capable of making by a direct effort of the will, we find that they are all of such a kind that through them the two images of an external object are brought upon corresponding parts of the two retinas; conversely the movements which could be effected by the contractions of this or that ocular muscle, but the effect of which would be to bring the two images on to parts of the retina which do not correspond, are the movements which our unassisted will cannot carry out.

In an earlier part of the work (§ 643) we insisted at some length on the important share taken by sensations, or at least by afferent impulses, in the coordination of motor impulses; and the movements of the eye illustrate this in a very marked degree. All the various movements of the eye are dependent on visual sensations. The issue of each efferent motor volitional impulse is dependent on afferent visual impulses. In order to move our eyes, we must either look at or for an object; when we wish to converge our axes, we look at some near object real or imaginary, and the convergence of the axes is usually accompanied by all the conditions of near vision, such as increased accommodation and constriction of the pupil. And so with other ocular movements. Above all, the careful selection of this or that ocular muscle, the extent to which it is to be thrown into contraction, its accompaniment by the contraction of other ocular muscles and the due coordination of all the several contractions—all these things are so determined by visual sensations that the two images of each object looked at fall on corresponding parts of the two retinas.

A little reflection will shew how large an amount of coordination must thus take place in daily life, how in the various movements of the eye there must be, so to speak, the most delicate picking and choosing of the muscular instruments. When we look at an object to the right, since we thereby turn the right eye to the temporal side, and the left eye to the nasal side, we throw into action the external rectus of the right eye and the internal rectus of the left; and similarly when we look to the left we use the external rectus of the left and the internal rectus of the right eye. On the other hand when we look at a near object, and therefore converge the visual axes, we use the internal rectus of both eyes; and when we look at a distant object, and bring the axes from convergence towards parallelism, we use the external rectus of both eyes. Or to take another instance. Suppose the eyes, to start with, directed for the far distance, and that it is desired to direct attention to a nearer point lying in the visual line of the right eye. In this case no movement of the right eye is required; all that is necessary is for the left eye to be turned to the right, that is, for the internal rectus of the left eye to be thrown into action. But in ordinary movements the contraction of this muscle is always associated with either the external rectus of the right eye, as when both eyes are turned to the right, or the internal rectus of that eye, as in convergence; the muscle is quite unaccustomed to act alone. This would lead us to suppose that in the case in question the contraction of the internal rectus of the left eye is accompanied by a contraction of both the external and the internal rectus of the right eye, keeping that eye in lateral equilibrium. And the peculiar oscillating movements seen in the right eye, as well as the sense of effort in the right eye which is felt by the person, support this idea. We need not multiply these instances; it must be sufficiently obvious that a very large amount of coordination takes place in the daily use of our eyes.

§ **793.** Such a coordination involves the existence of what, to continue the use of a term which we have previously used, we may call a coordinating nervous mechanism. The coordinated efferent impulses issue from one or more of the nuclei of the three cranial nerves concerned, namely the sixth, the fourth, and the third. The afferent visual impulses taking part in the coordination, we have in an earlier part of this book (§ 669) traced to the primary visual centres, and thence to the occipital cortex. The volitional impulses themselves are we have seen (§ 655) connected in some way or other with an area of the cortex lying in the monkey in the frontal lobe, in the neighbourhood and in front of the precentral fissure (Figs. 133, 134), and probably in man occupying a corresponding position. How are these three factors of the whole nervous action brought to bear the one on the other? When it is remembered how complex and delicately balanced are the movements in question, probably the most intricate and the most delicately balanced of all the movements of the body, it will readily be understood how difficult is the answer to such a question. Stimulation of the cortical areas for movements of the eyes leads as might be expected to bilateral movements, to movements of both eyes; but, so far as results hitherto obtained shew, the movements are bilateral in a special manner. The most common effect of stimulating the cortical area is a lateral movement of both eyes in the same direction towards the opposite side, a conjugate lateral deviation of both visual axes towards the opposite side. For instance, when the cortical area of the left hemisphere is stimulated, the visual axes of both eyes are turned to the right, the external rectus of the right eye and the internal rectus of the left eye being thrown into contraction by impulses passing down the right sixth nerve and left third nerve; the efferent impulses therefore cross in the case of one nerve but not in the case of the other. Similarly, when the right hemisphere is stimulated, impulses pass down the right third nerve and left sixth nerve. Stimulation of the occipital region (§ 671) also leads to a similar conjugate turning of both visual axes to the opposite side, accompanied in certain cases by a raising or lowering of the visual axes. Lateral deviation towards the side of the cortex stimulated only occurs, and that indefinitely, when the muscles concerned in moving the eyeballs to the opposite side have been divided. Under these conditions, however, upward and downward movements of the eyeballs on cortical stimulation undoubtedly occur.

By means of experiments of this kind it has been concluded that the contraction of one ocular muscle, or of one set of ocular muscles, is accompanied by inhibition of the antagonistic muscle or set of muscles (§ 598). In turning the eyes to the right there is reason to believe that the contraction of the right external rectus and of the left internal rectus is associated with inhibition and relaxation of the right internal rectus and of the left external rectus.

We have already (§ 671) urged that the ocular movements which result from the stimulation of the occipital region cannot be due to an indirect stimulation of the 'motor' frontal area, and that probably they are carried out through some special ties between the occipital cortex and the primary visual centres, especially the anterior corpus quadrigeminum; and in this relation, it is worthy of notice that ocular movements, similar to those obtained by stimulating the cortex, may be obtained by stimulating this part of the brain. Stimulation of these structures on one side leads to conjugate lateral movement of the visual axes to the opposite side, and it is stated that a more median stimulation leads to a downward movement of both sides with convergence, or in cases where convergence previously existed, to an upward movement with a return to parallelism. If on the other hand the stimulus is brought to bear directly on the nucleus of the third nerve the movements excited are said to be limited entirely to the eye of that side. From this we may infer perhaps that some, at least, of the coordination of which we are speaking, takes place in some part or other of the anterior corpora quadrigemina.

Lastly we may remark that the tract which we described (§ 634) as the posterior longitudinal bundle, contains fibres passing to the ocular nuclei, which may assist in coordination by serving as a tie between the several nuclei; and it has been urged that some of the fibres of this tract cross over from the sixth nucleus of one side and joining the tract of the opposite side pass to the third nucleus of the opposite side, thus affording an anatomical basis for what we have seen to be one of the most frequent associations in ocular movements, that of the external rectus of one eye with the internal rectus of the other eye. In connection with these nuclei it is worthy of note that while all the fibres proceeding from the sixth nucleus of one side pass into the nerve of the same side, some of the fibres issuing from the third nucleus appear to decussate (§ 623), and the whole of the fourth nerve (§ 622) crosses over from its nucleus before it leaves the brain. Yet there appears to be nothing special about the behaviour of the superior oblique to account for this feature.

### *The Horopter.*

§ **794.** When we look at any object we direct to it the visual axes, so that when the retinal image of the object is small, the 'corresponding' parts of the two retinas, on which the two images of the object fall, lie in their respective foveæ centrales. But while we are looking at the particular object the images of other objects surrounding it fall on the retina surrounding the fovea, and thus go to form what is called indirect vision. And it is

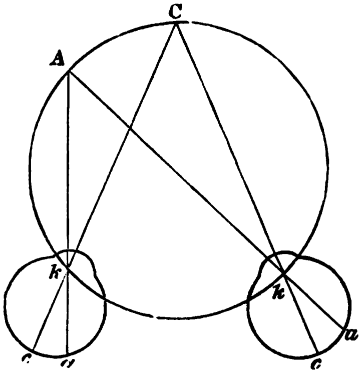

FIG. 167. DIAGRAM ILLUSTRATING A SIMPLE HOROPTER.

When the visual axes converge at *C*, the images *a a* of any point *A* on the circle drawn through *C* and the nodal points *k k*, will fall on corresponding points.

obviously of advantage that other images, besides that of the object to which we are specially directing our attention, should fall on 'corresponding' parts in the two eyes. Were it not so, while our vision of the particular object would be single, our vision of all its surroundings would be double; and this, at least in certain cases, would be confusing. For, even when we are concentrating our attention on a particular object, we are still conscious of its surroundings, and besides, our appreciation of any image falling on the fovea is influenced by impressions which we are at the same time receiving from other parts of the retina.

Now for any given position of the eyes there exists in the field of sight a certain line or surface of such a kind that the images of the points in it all fall on corresponding points of the retina. A line or surface having this property is called a Horopter. The horopter is in fact the aggregate of all those points in space which, in any given position of the eyes, are projected on to corresponding points of the retina; hence its determination in any particular case is simply a matter of geometrical calculation. In some instances it becomes a very complicated figure. The case whose features are most easily grasped is that of a circle drawn in the plane of the two visual axes through the point of the convergence of the axes and the nodal points of the two eyes such as is shewn in Fig. 167. It is obvious from geometrical relations that the two images of any point in such circle, the rays from which can enter the two pupils and fall on the two retinas, will fall on corresponding points of the two retinas. When we study the various horopters of the several positions which the two eyes can take up, we find that the characters of the horopter are adapted to the needs of our daily life. Thus in the position assumed by the two eyes when we stand upright and look at the distant horizon the horopter is (approximately, for normal emmetropic eyes) a plane drawn through our feet, that is to say, is the ground on which we stand; the advantage of this is obvious.

Nevertheless, in most positions of the eyes a large number of the images which make up the binocular visual field do not lie on any horopter, do not fall on corresponding points, and give rise not to one sensation only but to two sensations differing to a certain extent from each other. A great deal of what we see is seen double by us, we receive from many objects two unequal impressions; but the inequality chiefly serves to give an appearance of "solidity" to the objects, to assist in our judgment of distance and solidity. To the consideration of these and other visual judgments as well as of some other psychological features of vision we must now turn.

## SEC. 12. ON SOME FEATURES OF VISUAL PERCEPTIONS AND ON VISUAL JUDGMENTS.

**§ 795.** We may now turn our attention to some of those differences between the features of external objects and our perception of them which are more distinctly of psychological origin; but since the purpose of this work is physiological and not psychological we must be content to treat them very briefly.

Taking first of all the general features of the field of vision, we find psychical processes entering largely even into these. As we have incidentally seen, the sensations which an object excites are very different according as the object is in the central or in the peripheral region of the field of sight. Two parts of the object sufficiently far apart to give rise to two sensations in the former case may give rise to one sensation only in the latter case; and the colour sensations excited by the same object may be widely different in the two cases. If we picture to ourselves the group of sensations excited by the image of an object, such as a flower, when the image falls on the fovea, and compare that group with the group of sensations excited by the same flower when the image of it falls on the periphery of the retina, supposing the comparison to be made before the sensations are moulded into psychical perceptions, the two groups would appear to belong to very unlike objects. Moreover, when we use both eyes, the images of some of the objects in the field of sight are falling on both retinas, while others are falling on one retina only, and of those which fall on both retinas, some lie on corresponding points, so that the sensations of the two eyes are blended, while others, not lying in the horopter, give rise to sensations in one eye different from those in the other. Could we become aware of the crude sensations which go to make up our field of vision, they would appear as a heterogeneous medley. But in the field of vision of which we are actually aware, that in which the crude sensations have by psychical operations been moulded into perceptions, we do not recognize the various discrepancies of which we are speaking; the field of vision is homogeneous. When we look at a landscape we are not aware that objects on the far left or far right hand are producing sensations in a way very different from that in which objects directly in the line of vision are producing sensations; it is only by special analysis that we become acquainted with the properties of the peripheral retina. In actual vision the activities of the central retina by virtue of psychical processes dominate those of the periphery. Conversely though, as we have said, when we wish to see anything very distinctly we habitually make use of the central retina; yet nevertheless in ordinary vision, at the same time that we are thus making use of the central retina we are also receiving impressions from the whole of the rest of the retina within the field of vision, and these more or less peripheral impressions influence to a certain extent the psychical effect of the central sensations. Our perception of an object, such as a flower, is not the same when we look at it as a part of a landscape, making use of the whole field of vision, as when we look at it through a tube or otherwise in such a way as to exclude peripheral vision; the flower in the latter case seems much more brilliant, and more highly coloured. Some of the effect in this case may be physiological and due to retinal events, but the greater part is psychical. The influence of psychical processes is probably also illustrated by the experience that, if on turning our back on a landscape, we bend the body so as to get a view of the landscape backwards between the legs, all the objects seem to have an unusually brilliant colouring.

A striking difference between the objective field of sight and the subjective field of vision is illustrated by the fact that, though, as we have seen, that part of the retina which corresponds to the entrance of the optic nerve is quite insensible to light, we are conscious of no corresponding blank in the field of vision. When in looking at a page of print we so direct the visual axis that some of the print must fall on the blind spot, no gap in the print is perceived; we have to take special measures (§ 770) to discover the existence of the spot. We could not expect to see a black patch, because what we call black is the absence of the sensation of light from structures which are sensitive to light; we must have visual organs to see black. But there are no visual organs in the blind spot, and consequently we are in no way at all affected by the rays of light which fall on it. By psychical operations we "fill up," as it is said, the vacancy caused by the blind spot, so that there is in our subjective field of vision no gap corresponding to the gap in the retinal image; we treat the sensations coming from two points of the retina lying on opposite margins of the blind spot as if they were sensations excited in two points lying close together, thus preserving the continuity of the field of vision between them. Concerning the particular psychical actions by which this is carried out, and concerning the special effects which are produced when an object in the field of sight passes into the region of the blind spot there has been much discussion; but into this we cannot enter here.

In ordinary vision, the existence of the blind spot is of little moment. Since it lies outside the region of distinct vision, and since moreover in each movement of the eye the image of a fresh part of the external world falls upon it, the errors to which it may lead are not serious even when we use one eye only. The deficiency is further remedied by the use of two eyes, since, the two blind spots being each on the nasal side, the image of an object will not fall on both blind spots at the same time. Other smaller or accidental imperfections in one or both eyes are similarly remedied by the use of two eyes.

§ **796.** Turning now to the psychical processes connected with the perception of particular objects, we find these to be very complex. Some of them relate to the very formation of the perception out of the sensations which the object excites, and are often of such a kind that the perceptions which they influence so distinctly fail to correspond with the actual objects that the lack of correspondence can in many cases be demonstrated: such erroneous perceptions are often spoken of as "illusions." In other cases the psychical processes relate to a further mental action by which we form judgments as to the features of external objects. It is not easy however always to draw a line between a 'visual judgment,' such as that involved in forming a conclusion as to the size of an external object, and what may be called a mere 'modified perception,' as when a line appears to us shorter or longer than it really is. We may be content here to treat them all together.

The complexity of the psychical processes in question comes about in various ways. On the one hand the characters of a perception are determined not alone by the sensations which actually give rise to it but also by the psychical conditions remaining as the effect of former like sensations. In the formation of perceptions and judgments, suggestions and associations play their part; so that each perception, while it adds to, is also in part the result of our 'experience.' A simple illustration of this is seen in some of the effects of colour. Blue colours, as we have seen, predominate in a dim light such as that of evening, of moonlight, or of winter, whereas reds and yellows are marked in a bright light such as that of full sunshine or of a summer's day. Hence, when a landscape is viewed through a yellow glass, the yellow hue suggests to the mind bright sunlight and summer weather, although the actual illumination which reaches the eye is diminished by the glass. Conversely when the same landscape is viewed through a blue glass the idea of moonlight or winter is suggested. And many other instances might be given in which the appreciation of the present is moulded by the experience of the past.

Other influences also, such for instance as sensations of touch, and sensations derived from movements of the eyes, may take part in the psychical processes in question. The mere visual sensations which external objects excite, the immediate and direct effects of the visual impulses, form after all but a small part of what we call our vision. Such sensations and other like sensations derived through other senses are to us but symbols of things, upon which the mind puts its own interpretation. But into these matters we cannot enter here. We must confine ourselves to certain common facts concerning perceptions, illusions and visual judgments, and more especially to those which relate to the size and distance of external objects and to the characters of form which are indicated by the word "solidity."

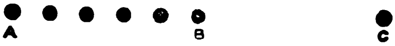

Fig. 168.

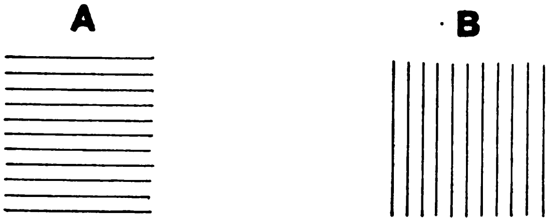

Fig. 169.

§ **797.** *Appreciation of apparent size.* The foundation of our judgment of the size of any object is the size of the retinal image of the object. We can distinguish a sensation involving a large retinal area from one involving a small area, and in the region of distinct vision can appreciate even small differences; this is of course only an exercise of the power of localization. We have seen however that, even in the case of a simple and single sensation such as that of a white patch on a black ground, the sensation does not correspond exactly to the objective stimulation of the retina; the white patch through irradiation § 780 appears larger than it really is. When we come to deal with more complex groups of sensations we find that over and above any such physiological modifications of the sensations, the psychical processes mentioned above affect our perceptions and judgments of size, often giving rise to illusions. If a line such as *AC*, Fig. 168, be divided into two equal parts *AB*, *BC*, and *AB* be divided by distinct marks into several parts, as is shewn in the figure, while *BC* be left entire, the distance *AB* will always appear greater than *CB*. The retinal images of the spaces from *A* to *B* and from *B* to *C* are equal and the corresponding primary visual sensations are also equal, but the mental appreciation of *A B* is interfered with by the concurrent sensations of the several intervening dots and intervals, and this leads to a mental exaggeration of the interval between *A* and *B*. So also, if two equal squares (Fig. 169) be marked, one with horizontal and the other with vertical alternate dark and light bands, the former will appear higher, and the latter broader, than it really is. These illusions have also been referred to the influence of movements of the eyes. It has been supposed that the eye in passing from *A* to *B* in Fig. 168 encounters more resistance than in passing from *B* to *C*, and that this gives an idea of greater distance in the former case. On the other hand, attempts have been made to refer these illusions to a purely physiological factor, the curvature of the retina. Again, when a short person is placed side by side with a tall person, the former appears shorter and the latter taller than each really is. By reason of somewhat obscure psychical processes two perfectly parallel lines or bands, each of which is crossed by slanting parallel short lines (Fig. 170), will appear not parallel, but diverging or converging according to the direction of the cross-lines; the direction of the cross-lines affects our perception of the distance between the parallel lines. This and other allied illusions have been referred to the erroneous estimation of angles. We tend to overestimate acute angles and to underestimate obtuse angles. These illusions in the perception of angles have, like the illusions considered above, been referred to the influence of the curvature of the retina, but their nature is at present very doubtful.

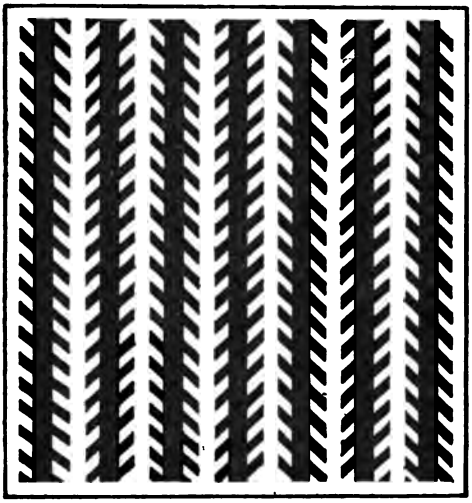

FIG. 170.

§ **798**. *Perception of distance and actual size.* The size of the retinal image gives us by itself a measure not of the real size but only of the apparent size of the object. The size of the retinal image will depend on the distance of the object and on the dioptric arrangements of the eye; with the same dioptric arrangements it will depend on the angle subtended by the diameter of the object, and this may be the same for a small object near as for a large object far off. In order to form a judgment as to the actual size of an object, we must adjust our perception of the apparent size by means of a judgment of the distance at which the object is placed; and here the great use of two eyes comes in.

Even with one eye we can, to a certain extent, form a judgment not only as to the position of the object in a plane at right angles to our visual axis, but also as to its distance from us along the visual axis. It has been supposed that we do this by means of our accommodation, that the muscular sense of the effort of accommodation, or that arising from relaxation of accommodation, enables us to form a judgment whether the object is far or near. It is however very doubtful whether such muscular sensations are of any influence. And, indeed, all monocular judgments of distance are subject to much error. Everyone who has tried to thread a needle or to pour out a glass of wine without using both eyes, knows such errors. It is probable that such power of estimating distance as exists in monocular vision is dependent in some way on psychical factors.

In the same way, in vision with two eyes, it has been supposed that the sensations arising from accommodation are assisted by others arising from the movements of convergence and divergence of the eyeballs. This again is very doubtful. We know that we are perfectly well able to estimate distance during instantaneous exposure; in such cases movements of the eyes can have no influence. The same may also be shewn by means of a simple experiment, in which the observer looks through a tube at a fixed point, while objects are allowed to fall through the field of vision. It is found that, using two eyes, one is perfectly well able to distinguish whether the falling object is nearer or farther than the fixed point, although the time during which the object is exposed is too short to allow a movement of the eyes to take place. When, on the contrary, only one eye is used, it is found that one is wholly unable to give correct estimates of distance. This experiment seems to shew that there exists a binocular mechanism of some kind which enables us to estimate distance independently of movements of the eyes.

As to the nature of this binocular mechanism, it is not so easy to speak with certainty. When our eyes are directed to a given point, all other points lying in the horopter will stimulate corresponding points of the retina, and will appear at the same distance from the eyes. Points in space which lie outside the horopter will stimulate disparate points, but the nature of this disparate stimulation will vary according as the points in question are nearer or farther than the horopter. If the amount of disparate stimulation is sufficient, the points would be seen double, and the double images of points nearer than the horopter would be crossed (§ 787) while those of points beyond the horopter would be uncrossed. The most feasible view of the binocular mechanism is that our perception whether an object is nearer or farther than the fixation point (or horopter), depends so far as it is a physiological process on this difference in the nature of the retinal stimulation, even though no double images are seen. Even accepting this, however, as the physiological basis of our perception of distance, there is no doubt that the process is also affected to an enormous extent by factors of a purely psychological nature.

The judgment of size is, as we have said above, closely connected with that of distance. The real size of the object can be inferred from the apparent size, that is to say from the size of the retinal image, only when the distance of the object from the eye is known. Thus when an object gives rise to a retinal image of a certain size, that is to say has a certain apparent size, we estimate the distance from us of the object giving rise to the image, and upon that come to a conclusion as to its real size. Conversely, when we see an object, of whose real size we are otherwise aware, or are led to think we are aware, our judgment of its distance is influenced by its apparent size. Thus when part of our field of vision is occupied by the image of a man, knowing otherwise the ordinary size of a man, we infer, if the image be very small, that the man is far off. The reason of the image being small may be because the man is far off, in which case our judgment is correct; it may be, however, because the image has been lessened by artificial dioptric means, as when the man is looked at through an inverted telescope, in which case our judgment becomes an illusion. So also a picture on a magic lantern screen when gradually enlarged seems to come forward, when gradually diminished seems to recede. In these cases the influence of any physiological factors which may exist is thwarted by the more direct influence of the association between size and distance. An instructive illusion of a similar kind is produced by developing in the eye a strong negative image (§ 782) and projecting the image on to a screen which is made to move backwards and forwards, or is alternately inclined at various angles; the negative image appears to change in size and shape, although it is itself absolutely subjective in nature and wholly independent of the movements of the screen.

The complex reaction on each other of judgments as to distance and size is illustrated by the experience that an object such as a person looks unnaturally large when seen in a fog; being seen indistinctly, he is judged to be farther off than he really is, and so appears larger than he naturally would do at the distance at which he is supposed to be; and we are similarly influenced by the greater or less brightness or saturation of colours. Conversely, distant mountains when seen distinctly in a clear atmosphere appear small, because on account of their distinctness they are judged to be nearer than they really are. The indistinctness of the image of the moon or sun when seen on the horizon, similarly contributes to its appearing larger than when seen in the zenith; our judgment however is probably in this case also due to our being better able to compare the moon or sun with terrestrial objects. We seem moreover in this matter to be especially influenced by our conception (which is itself an illustration of the subject we have in hand) that the vault of the heavens is flatter than it really is; the zenith appears to be less distant than the horizon; a geometric construction will shew that a body of the same size placed at different parts of the real (spherical) vault will appear greater near the horizon than near the zenith of the flatter, apparent, vault. An amusing illustration of visual judgments may be obtained by asking a number of persons in succession what they regard as the size of the moon in mid heavens. Even making allowance for dioptric differences in individual eyes the size of the retinal image of the moon must be about the same in all eyes. And yet while some persons will be found ready to compare the moon in mid heavens with a threepenny piece, others will liken it to a cart-wheel, and others will make intermediate comparisons.

§ **799**. *Perception of solidity.* When we look at a small circle all parts of the circle are at the same distance from us, all parts are equally distinct at the same time, whether we look at it with one eye or with two eyes. When, on the other hand, we look at a sphere, the various parts of which are at different distances from us, the binocular mechanism makes us aware that the various parts of the sphere are unequally distant; and from that we form a judgment of its solidity. As with distance of objects, so with solidity, which is at bottom a matter of distance of the parts of an object, we can form a judgment with one eye alone; but our ideas become much more exact and trustworthy when two eyes are used. We are further much assisted by the effects produced by the reflection of light from the various surfaces of a solid object, and the shadows cast by its raised parts; so much so, that raised surfaces may be made to appear depressed, or *vice versâ*, and flat surfaces either raised or depressed, by appropriate arrangements of shadings and shadow, and in monocular vision our perception of solidity probably altogether depends on these effects.

Binocular vision, moreover, affords us a means of judging of the solidity of objects, inasmuch as the image of any solid object which falls on to the right eye cannot be exactly like that which falls on the left, though both are combined in the single perception of the two eyes. Thus, when we look at a truncated pyramid placed in the middle line before us, the image which falls on the right eye is of the kind represented in Fig. 171 R, while that which falls on the left eye has the form of Fig. 171 L; yet the perception gained from the two images together corresponds to the form of which Fig. 171 B is the projection. Whenever we thus combine in one perception two dissimilar images, one of the one, and the other of the other eye, we judge that the object giving rise to the images is solid.

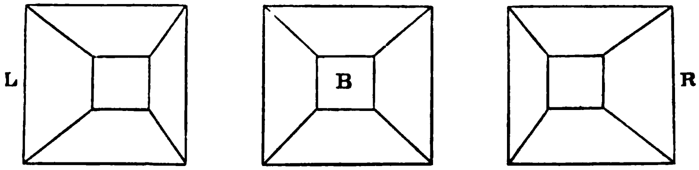

FIG. 171.

This is the simple principle of the stereoscope, in which two slightly dissimilar pictures, such as would correspond to the vision of each eye separately, are, by means of reflecting mirrors, as in Wheatstone's original instrument, or by prisms, as in the form introduced by Brewster, made to cast images on corresponding parts of the two retinas so as to produce a single perception. Though each picture is a surface of two dimensions only, the resulting perception is the same as if a single object, or group of objects, of three dimensions had been looked at.

It might be supposed that the judgment of solidity which arises when two dissimilar images are thus combined in one perception, was due to the fact that all parts of the two images cannot fall on corresponding parts of the two retinas at the same time, and that therefore the combination of the two needs some movement of the eyes. Thus, if we superimpose R on L (Fig. 171), it is evident that when the bases coincide the truncated apices will not, and *vice versâ;* hence, when the bases fall on corresponding parts, the apices will not be combined into one image, and *vice versâ;* in order that both may be combined, there must be a slight rapid movement of the eyes from the one to the other. That, however, no such movement is necessary for each particular case is shewn by the fact that solid objects appear as such when illuminated by an electric spark, the duration of which is too short to permit of any movements of the eyes. If the flash occurred at the moment that the eyes were binocularly adjusted for the bases of the pyramids, the two summits not falling on exactly corresponding parts would give rise to the perceptions of two summits, and the whole object ought to appear confused. That it does not, but, on the contrary, appears a single solid, must be the result, partly of psychical operations, partly of the action of the binocular mechanism for estimating differences of distance.

As we have seen, in any one position of the two eyes, only a small portion of the field of sight lies in the horopter and falls on corresponding points of the two retinas. Most of the objects in a scene on which we look give rise to dissimilar images in the two eyes; and we attribute solidity to them by reason on the one hand of the binocular mechanism, and on the other hand of the psychical processes just mentioned. Conversely the same processes which thus give rise to apparent solidity assist us in forming judgments of distance.

§ **800.** If the images of two surfaces, one black and the other white, are made to fall on corresponding parts of the eye, so as to be united into a single perception, the result is not always a mixture of the two impressions, that is a grey, but, in many cases, a sensation similar to that produced when a polished surface, such as plumbago, is looked at: the surface appears brilliant, is said to have a "lustre." The reason probably is because when we look at a polished surface the amount of reflected light which falls upon the retina is generally different in the two eyes; and hence we associate an unequal stimulation of the two retinas with the idea of a polished lustrous surface.

We may in this connection refer to what is known as "the struggle or rivalry of the two fields of vision," though the matter is one of sensations and not of judgments or intricate psychical processes. When the impressions of two colours are united in binocular vision, the result is in many cases a mixture of the two colours, as when the same two impressions are brought to bear together at the same time on a single retina, but there is often a struggle between the two colours, now one, and now the other, becoming prominent, intermediate tints however being frequently passed through. This may arise from the difficulty of accommodating at the same time for the two different colours (§ 735); both eyes will be accommodated at the same time and to the same degree, but if two eyes, one of which is looking at red, and the other at blue, be at one moment both accommodated for red rays, the red sensation will overpower the blue, while if at another moment they are both accommodated for blue, the blue will prevail. It may be however that the tendency to rhythmic action, so manifest in activity of other simpler forms of living matter makes its appearance also in the cerebral changes involved in binocular vision.

## SEC. 13. THE NUTRITION OF THE EYE.

§ **801.** The main blood vessels of the eye are, as we have incidentally seen, the arteria centralis supplying the retina, and the (posterior) ciliary arteries supplying the choroid, ciliary processes and iris, the vessels going to the choroid being called the short ciliary arteries, and those reaching forward to the ciliary processes and iris, the long ciliary arteries. From the arteria centralis retinæ the blood is returned by the vena centralis, while the venæ vorticosæ of the (posterior) ciliary veins gather up the blood of both the long and the short (posterior) ciliary arteries. These two systems communicate to some extent with each other by anastomoses at the entrance of the optic nerve, but on the whole are independent.

In addition to the above, the anterior ciliary arteries pass to the eyeball with each of the four straight ocular muscles, supplying the front part of the sclerotic as well as the edge of the cornea, and sending through the sclerotic 'perforating' arteries to end in the iris, ciliary processes, and front part of the choroid, and so join the system of the posterior ciliary arteries. Corresponding to these anterior ciliary arteries are veins which make their way back to the ocular muscles, and the roots of which are especially connected with the circular canal of Schlemm (§ 717). Further, the edge of the cornea is in addition supplied by conjunctival blood vessels.

The blood-supply of the various parts of the eye is therefore somewhat as follows. The inner layers of the retina are supplied in a direct manner by the arteria centralis retinæ, but the outer layers together with the pigment epithelium in an indirect manner by the close set choroidal network "choriocapillaris" of the posterior ciliary arteries. The choroid proper, that part which serves as an investment to the retina and specialized pigment epithelium, is supplied by the short (posterior) ciliary arteries; but the front ciliary part of the choroid, together with the ciliary processes and iris, receives blood from the long (posterior) ciliary arteries, and also from the anterior ciliary arteries. The cornea is supplied by the conjunctival as well as by the anterior ciliary arteries, the blood vessels as we have said extending a short distance only within the circle of the corneal circumference, while the scanty supply of the sclerotic is furnished in the front part of the eyeball by the anterior and in the hind part by the posterior ciliary arteries.

The nutritive supply of the lens, with its capsule, and of the vitreous humour is an indirect one, by means of lymph; the anterior surface of the former is bathed by the aqueous humour; the lymph streams in the vitreous humour, of which we shall speak immediately, furnish that substance with the scanty nourishment it needs, and sweep by the posterior surface of the lens.

§ **802.** In speaking of the movements of the pupil we referred to vaso-motor changes in the eye. So far as our present information goes, we have evidence chiefly of vaso-constrictor fibres which passing from the sympathetic to the ciliary ganglion (§ 725) reach the posterior ciliary arteries by the short ciliary nerves; but there are facts which seem to shew that the fifth nerve supplies vaso-dilator fibres through the ophthalmic branch.

The separate distribution of the short ciliary arteries to the hinder part of the choroid investment which is busy with the nourishment of the retina and which takes little or no share in the movements of accommodation, and of the long ciliary arteries to the front part of the investment which, as iris, ciliary processes and muscle, and front part of the choroid itself, is concerned in the movements of the pupil and of accommodation, suggests that a corresponding separate distribution of vaso-motor nerves also exists; but we have no exact experimental evidence of this.

We saw in speaking of the brain (§ 700) that clear evidence of the cerebral vessels being subject to vaso-motor influences was wanting; and in this respect once more the retina behaves like a part of the brain. Though by help of the ophthalmoscope changes of calibre in the retinal vessels can easily be observed, we have as yet no decisive proof that such changes can be brought about by vaso-motor nerves acting directly on the arteria centralis retinæ. The changes which are observed seem to be determined not by the greater or less contraction of the muscular coat of the retinal vessels themselves, but by the pressure to which the blood in the vessels is subjected, and that may be varied by many extraneous causes.

## *The Lymphatics of the Eye.*

§ **803.** Though the lymph in the large serous cavities may be considered to play a mechanical part inasmuch as it facilitates the movements of the viscera, and though in such a tissue as the skin, the lymph in the cavities and vessels of the dermis may similarly perform a mechanical task in assisting to give at once firmness and suppleness to the skin, yet over the body at large the function of the lymph is preeminently a nutritive one, and its mechanical duties are insignificant. As regards the eye the case is different. The eyeball is broadly speaking a shell filled with fluid, the aqueous and vitreous humours; and for the various functions of the eye it is necessary that this shell should be filled to a certain extent, should be tense to a certain degree, not more and not less; and this fulness, this "intraocular tension,' which is considerable, probably much higher than the ordinary pressure in the lymph-spaces of the body at large, is provided by the lymphatic arrangements. If the retina were not adequately supported by the vitreous humour, if it could flap about or in any way alter its curvature, the dioptric arrangements of the eye would be upset; if the vitreous humour at one time shrank, at another expanded, the movements of accommodation could not be carried on; if the aqueous humour were now abundant, now scanty, the movements of the pupil would become irregular and uncertain; and if the whole globe were so flabby as to give way under the pull of each ocular muscle, the delicate movements of the eyeball on which we lately dwelt would become impossible. Hence the lymphatics of the eye have a double importance, inasmuch as they not only, as elsewhere, assist in maintaining the due nutrition of the several tissues, but also in a mechanical way help to make the eye an adequate dioptric instrument. In accordance with this double duty we find a special lymph apparatus added to the more general lymphatic arrangements such as exist elsewhere.

As belonging to the more general arrangements we may note the following. The lymph-spaces of the cornea pass at the margin of the cornea into the lymphatic vessels of the conjunctiva. The scanty lymph-spaces of the sclerotic pass at the extreme front into the conjunctival lymphatics, but elsewhere are continuous either on the inner surface with the perichoroidal lymph-spaces, or on the outer surface and that more freely, with the large lymphatic *Tenonian cavity*. Tenon's capsule is a loose thin investment of connective tissue lying between the sclerotic and the ocular muscles and forming sheaths round the tendons of the latter. Between the looser capsule and the denser sclerotic is a large irregular lymphatic cavity bearing the above name. The perivascular and other lymph-spaces of the choroid join the perichoroidal spaces, which in turn communicate with the Tenonian cavity by lymph-spaces or lymphatics accompanying the ciliary veins and to some extent the ciliary arteries as these pierce the sclerotic. The Tenonian cavity itself joins a large lymphatic cavity surrounding the optic nerve, 'the supravaginal' cavity, whence the lymph is carried away by the ordinary lymphatics of the orbit.

The perivascular and other lymph-spaces of the retina are in connection with the lymph-spaces of the optic nerve, which in turn join the subarachnoid space of that nerve, and this is continuous with the corresponding space in the brain. There appear to be also paths uniting these lymphatics of the retina and optic nerves with the perichoroidal spaces and Tenonian cavity, and so with the external lymphatic system.

§ **804.** In the special lymph apparatus the ciliary processes, the iris, the aqueous humour and the vitreous humour are concerned.

*The aqueous humour.* We have more than once spoken of the anterior chamber as a lymphatic cavity; nevertheless the aqueous humour contained in it differs greatly from ordinary lymph. Not only does it contain much more water, the total solids being not much more than 1 p.c. (1·3 p.c.) but also the relative proportion of the solids between themselves is different from that of lymph, and special substances are present in it. The proteids are particularly scanty, not more than about ·1 p.c.; these are serum-albumin, globulin, and apparently fibrinogen. Inorganic salts are present in about the same proportion as in blood and lymph, viz. ·8 p.c.; and these, chiefly sodium chloride, with an unusual proportion (·4 p.c.) of so-called extractives, furnish nearly all the solid matter. Among these extractives is a substance which reduces cupric solutions but which is not a sugar, though its exact nature is as yet unknown; urea and sarcolactic acid (in some combination) are also said to be, at least often, present. The reaction is neutral or faintly alkaline.

Like the 'serous fluid' in the large serous cavities and the cerebrospinal fluid in the cavities of the central nervous system, the aqueous humour comes and goes; the particular fluid which at any given moment is present in the eye has not always been there; some of the fluid is continually passing away and fresh fluid continually arriving. If fluid be withdrawn from the anterior chamber by puncture of the cornea, the chamber is soon refilled; indeed, under certain circumstances, a considerable quantity of fluid may be drained away from the chamber, fresh fluid taking the place of that which escapes. And, though under normal conditions the quantity of aqueous humour is fairly constant, the fluid may be in excess or may be deficient, and the one phase may pass into the other. The question therefore arises, Whence comes the fluid and whither does it go?

The characters of aqueous humour just given shew that in many respects it resembles cerebro-spinal fluid though differing in several features. That fluid, we have seen reason to believe (§ 694), is in part at all events furnished by the choroid plexuses, by a process which presents some analogies with the act of secretion. And the resemblance between the ciliary processes and the choroid plexuses, for both are vascular folds of pia mater covered with epithelium derived from the lining of the primitive medullary canal, suggests that the former furnish the aqueous humour in some such way as the latter furnish the cerebro-spinal fluid. There is a certain amount of experimental evidence in favour of this view, for when such a substance as fluorescin, which can be detected by the greenish tinge which it gives to the fluids and tissues, is injected into the body, into the subcutaneous connective tissue or peritoneal cavity for instance, not only does it speedily appear in the aqueous humour, but the ciliary processes are said to be the parts of the eye in which its presence may be first detected. It may be urged that, unlike the epithelium covering the choroid plexuses, the pars ciliaris retinæ bears no distinctive histological indications of secretory activity; but, as we shall presently have occasion to point out, a wholly analogous layer of epithelium, that lining the cavities of the internal ear, though possessing no marked secretory features, certainly furnishes, by an act very similar to secretion, a more or less lymph-like fluid, the so-called endo-lymph. The phrase 'secretion' however must not be strained. The somewhat specialized loose stroma of both the ciliary processes and iris undoubtedly contains in its meshes a large quantity of what we may suppose to be ordinary lymph; and what is intended by the above view is that while some of this lymph may pass by the perichoroidal spaces and so away as ordinary lymph, a much larger proportion passes on to the free surfaces abutting on the posterior and anterior chambers, and in so passing becomes modified in nature.

The fluid thus furnished by the ciliary processes makes its way, in the first place, into the posterior chamber; but though the iris, as we have seen (§ 722), lies close on the lens, there is undoubtedly a communication between the two chambers sufficiently free to allow fluid to pass readily from one to the other and so to fill the anterior chamber from the posterior. It is difficult to suppose that some of the lymph with which the sponge-like stroma of the iris is laden, does not find its way direct through the anterior surface of the iris into the anterior chamber; and such a transit would probably be assisted by the continual changes of the pupil. On the other hand the extent of surface furnished by the ciliary processes, which moreover also have the advantages of movement in each act of accommodation, is very large compared with that of the iris; hence we may probably with confidence conclude that the greater part of the aqueous humour is furnished by the ciliary processes, though the iris may contribute. We may add that probably the iridic contribution differs in nature from the rest, since the epithelium which the fluid has to traverse is a thin layer of flat epithelioid plates.

The answer to the question, How does the aqueous humour leave the anterior chamber? presents perhaps less difficulties. As we have seen (§ 717), the anterior chamber at the 'iridic angle' communicates freely with the spaces of Fontana, and these with the canal of Schlemm, which in turn is in direct connection with the radicles of the anterior ciliary veins. Since the ciliary muscle pulls on the tissue surrounding the canal of Schlemm it is possible, or even probable that the movements of accommodation help alternately to close and open the canal, and thus to pump its contents into the veins; by this means the exit of fluid from the anterior chamber is rendered less dependent on the relative pressures of the blood in the veins and of the fluid in the anterior chamber. By this channel the aqueous humour gains a ready, relatively direct, and short access to the blood-stream. And clinical experience shews that if this way be blocked an accumulation of aqueous humour results.

We may conclude then that the aqueous humour is a reservoir intercalated in a stream of a peculiar fluid which is passing from the ciliary processes through the small posterior and larger anterior chamber, the spaces of Fontana and the canal of Schlemm into the venous system. This reservoir on the one hand serves a mechanical purpose in preserving the natural form of the eye and in affording an adequate fluid bed for the movements of the iris, and on the other hand, by bringing new food material and carrying away waste products, enables the lens to carry out the slow and scanty metabolism necessary for its life.

§ **805**. For mechanical purposes the due condition of the vitreous humour is perhaps even more important than that of the aqueous humour. We have already (§ 720) called attention to the fact that the vitreous humour in spite of its being originally a plug of mesoblastic tissue, in adult life closely resembles the aqueous humour in its chemical features; and indeed it is practically an attenuated mesoblastic sponge through which is continually streaming, though at a slow rate, a fluid identical with or exceeding like to the aqueous humour. Through the optic disc the fluid of the vitreous humour has access to the lymph-spaces of the optic nerve; material injected into the pial sheath of the optic nerve finds its way through the optic disc into the vitreous humour passing along a 'central canal,' 'hyaloid canal' which remains after the disappearance of the prolongation of the arteria centralis retinæ (§ 703). And probably some of the fluid of the vitreous humour finds its way by this path into the subarachnoid space.

But the greater part of the fluid of the vitreous humour seems to belong to the same system as the aqueous humour. Fluids pass readily in some way or other through the suspensory ligament; fluid injected into the vitreous humour finds its way into the anterior chamber, and a block at the iridic angle leads to undue distension, not of the anterior and posterior chambers only, but of the whole globe of the eye; the pressures of the aqueous and vitreous humours are the same and vary similarly and concurrently. We have no satisfactory evidence that any large amount of fluid passes direct from the choroid through the retina, past the internal limiting and hyaloid membranes into the vitreous humour; as far as we know the whole of the lymph of the retina is carried away by the optic nerve in the manner mentioned above; and we must therefore conclude that the region of the zonule of Zinn serves as the door both for the entrance and exit of fluid, the circulation through the vitreous humour between its indistinct concentric lamellæ being secured by diffusion assisted by the movements of the eyeball.

This important flow of what we may call modified lymph, like that of the more ordinary lymph in other parts of the body, is determined in the first instance by the blood-flow, and we may apply to the eye the remarks which were made when (§ 302) we treated generally of the relations of lymph to blood-supply. Broadly speaking the intraocular pressure rises and falls with the general blood-pressure; the dim cornea and sunk eye that betoken the approaching end are due to the fall of blood-pressure which accompanies death. A local fall, preceded by a transient rise, may be brought about by stimulation of the cervical sympathetic, and a local rise by stimulation of the ophthalmic branch of the fifth nerve, stimulation of the third nerve having apparently little effect in either direction. We may add that, tempting as the view may seem that the lymph arrangements of the eye are under the direct control of the nervous system, we have no evidence that such is the case.

Concerning the influence of the nervous system on the general nutrition of the eye, and the disorders which follow upon section or injury to the fifth nerve we have already, in an earlier part of the work (§ 549), said all that at present we have to say.

## SEC. 14. THE PROTECTIVE MECHANISMS OF THE EYE.

§ **806**. The eye is protected by the two eyelids, each of which is strengthened and rendered firm by a curved plate of dense connective tissue called the tarsus (or incorrectly the tarsal cartilage), which is larger in the upper than in the lower eyelid. Elevation of the upper eyelid assisted by some depression of the lower eyelid is spoken of as "opening the eye"; depression of the upper eyelid assisted by elevation of the lower eyelid is spoken of as "shutting the eye." The latter movement is brought about by the contraction of the *orbicularis oculi*, a muscle of circularly disposed striated fibres placed beneath the skin of each eyelid and stretching also over the adjoining bony orbit. The muscle is governed by a branch of the seventh, facial nerve, and may be thrown into action as part of a reflex act or of a voluntary effort. When the facial nerve becomes incapable, through injury or disease, of carrying motor impulses, the eye can not be shut and remains widely open. There are some reasons however for thinking that the motor fibres for the orbicularis, though forming part of the facial nerve outside the brain, take origin within the brain, not from the facial nucleus but from the hind end of the third, oculo-motor nucleus. In the reflex contraction of the orbicularis, known as 'winking' or 'blinking,' which is so familiar as an almost typical reflex movement, but which in the waking hours is repeated so regularly, twice a minute or so, as to take on almost the characters of a rhythmic automatic act, the exciting afferent impulses are carried along the fibres of the fifth nerve distributed to the cornea and conjunctiva, and probably, but not certainly, pass some way down the ascending root (§ 621) of that nerve.

The eye is opened mainly by the raising of the upper eyelid through the contraction of the *levator palpebræ superioris*. This muscle, taking origin from the back of the orbit in company with the ocular muscles, is inserted into the upper surface of the tarsus of the upper eyelid, beneath the orbicularis. It is governed by a branch of the third nerve; hence injury or disease of this nerve is frequently the cause of a drooping of the upper eyelid and an inability to open the eye fully.

A portion of the tendon of the levator palpebræ closely united with an extension of the tendon of the superior rectus is inserted into the hinder part of the upper eyelid, where the conjunctiva lining it is about to be reflected over the eyeball; and a similar extension of the inferior rectus is similarly inserted into the lower eyelid. Hence a contraction of the superior rectus, while elevating the visual axis, at the same time raises somewhat the upper eyelid; and in like manner the inferior rectus, while depressing the visual axis, lowers the lower eyelid.

Between the main tendon of the levator palpebræ and the tendinous slip just mentioned lies a small bundle of plain, unstriated muscular fibres, which starting from the levator, ends in the hind border of the tarsus; it is sometimes spoken of as the middle insertion of the levator. A similar bundle of plain muscular fibres connects the insertion of the inferior rectus with the tarsus of the lower eyelid. These two small plain unstriated muscles appear to be governed by nervous filaments proceeding from the cervical sympathetic, stimulation of the cervical sympathetic leading to contraction of these muscles and so to a partial opening of the eye, and section of the same nerve preventing their being thrown into contraction and so contributing to closure of the eyelids. In some of the lower animals this closure of the eye upon section and opening upon stimulation of the cervical sympathetic is very distinct. In those animals which possess a third eyelid this retracts upon stimulation and prolapses upon section of the cervical sympathetic.

Stimulation of the cervical sympathetic also causes some protrusion, and section causes recession of the whole eyeball; this is seen at times in man in disease.

§ **807.** The conjunctiva which lines the ocular surface of the eyelids and is reflected from them over the eyeball, the line along which reflection takes place being spoken of as the *fornix conjunctivæ*, consists like the skin of the body of which it is a continuation, of an epithelium or epidermis resting on a dermis of connective tissue. It differs from the skin in the dermis being delicate and in the epidermis being thin with a tendency for the constituent cells to become columnar; hence it is sometimes spoken of as a "mucous membrane." On the ocular surface of the eyelids the conjunctiva is thrown into irregular ridges or imperfect and fused papillæ, giving rise to a satiny appearance; here the epithelium consists of several layers of cells, the uppermost of which are flattened. Over the fornix, the epithelium consists of two or three layers only, the cells in the uppermost layer being cubical or columnar; over the bulb the epithelium consists also of a few layers only, the upper cells being somewhat flattened and the dermis being thrown up into scattered papillæ.

Imbedded in the tarsus, stretching from the hind border to the free edge of the lid lies, in each eyelid, a row of thirty or fewer largely developed sebaceous glands (§ 437) the Meibomian glands. Sebaceous glands are also attached to the follicles of the eyelashes, and into the ducts of some of these open the glands of Moll, which have the structure of a sweat gland (§ 436). Small mucous glands are moreover found in the conjunctiva, especially in the neighbourhood of the fornix.

These several glands contribute to keep the surface of the eye and eyelids moist; but this is chiefly effected by the secretion of the lachrymal gland which is placed above the upper eyelid in the lateral region of the orbit, and which, imperfectly divided by an extension of the tendon of the levator palpebrarum into two masses, discharges its secretion by several ducts opening along the fornix conjunctivæ. Under ordinary circumstances the fluid thus secreted is carried away through the punctum lachrymale of the upper and of the lower eyelid, at the inner angle of the eye, into the lachrymal canaliculi, and so into the lachrymal sac, and finally into the cavity of the nose. When the secretion becomes too abundant to escape in this way it overflows on to the cheeks in the form of tears.

The structure of the lachrymal gland is in its main features identical with that of an albuminous salivary gland, or with that of the parotid, save that the epithelium of the ducts is never striated; it will be unnecessary to describe it in detail. In some animals a somewhat peculiar gland, the Harderian gland, lies in the inner (median) region of the orbit; this varies in structure in different animals, being in some a sebaceous gland united with a gland similar in structure to the lachrymal gland.

If a quantity of tears be collected, they are found to form a clear faintly alkaline fluid, in many respects like saliva, containing about 1 p.c. of solids, of which a small part is proteid in nature. Among the salts present sodium chloride is conspicuous.

The nervous mechanism of the secretion of tears, in many respects, resembles that of the secretion of saliva. A flow is usually brought about either in a reflex manner by stimuli applied to the conjunctiva, the nasal mucous membrane, the tongue, and the interior of the mouth, or more directly by emotions. Powerful stimulation of the retina by light will also cause a flow, as will electrical or other stimulation of any of the cranial or upper spinal afferent nerves. Venous congestion of the head is also said to cause a flow. The efferent nerves are the lachrymal and orbital branches of the fifth nerve, especially the former, stimulation of these causing a copious flow. It is said that stimulation of the cervical sympathetic will also cause a somewhat scanty flow of turbid tears, but on this point all observers are not agreed.

The chief use of the act of blinking is to keep the surface of the cornea moist, and so transparent; if the cornea be kept uncovered for a few minutes its dried surface soon becomes dim. But besides this, blinking undoubtedly favours the passage of tears through the lachrymal canaliculi into the lachrymal sac, and hence when the orbicularis is paralysed tears do not pass so readily as usual into the nose; but the exact mechanism by which this is effected has been much disputed. According to some authors the contraction of the orbicularis presses the fluid onwards out of the canals, which, upon the relaxation of the orbicularis, dilate and receive a fresh quantity. Others maintain that a special arrangement of muscular fibres keeps the canals open even during the closing of the lids, so that the pressure of the contraction of the orbicularis is able to have full effect in driving the tears through the canals.

# CHAPTER IV.

## HEARING.

### SEC. 1. ON THE GENERAL STRUCTURE OF THE EAR, AND ON THE STRUCTURE AND FUNCTIONS OF THE SUBSIDIARY AUDITORY APPARATUS.

**§ 808.** WE have seen that the eye consists on the one hand of the special modified epithelium, the retina, so constituted that light falling upon it gives rise to visual impulses in the optic nerve and thus to visual sensations in the brain, and on the other hand of a special dioptric mechanism, into the construction of which several tissues enter, and which is so arranged as to cause the rays of light to fall in a proper manner on the retina. In the ear we meet with a somewhat similar arrangement; we may recognize on the one hand a specially modified epithelium, which we may call the *auditory epithelium,* so constituted that the vibrations of matter, the rapidly alternating variations of pressure, which we call "waves of sound," generate in the auditory nerve connected with it auditory impulses, developed in the brain into auditory sensations; and on the other hand an acoustic apparatus so arranged that waves of sound are conducted in a proper manner to the auditory epithelium. Just as visual impulses can be excited by light only through the mediation of the retina, so auditory impulses can be excited by sound only through the mediation of the auditory epithelium; but here the analogy between the optic auditory nerves seems to end, for while as we have seen the optic nerve conveys, so far as we know, visual impulses only, we have reason to think (§ 642) that some fibres at least of the auditory nerve convey impulses which do not give rise to auditory sensations, but enter in a peculiar manner into the mechanism of coordinated movements.

The retina as we have seen is developed out of the optic vesicle, and the subsidiary dioptric mechanism is built up around the optic vesicle; and in a somewhat similar way the auditory epithelium is developed into an *otic vesicle*, and the subsidiary acoustic apparatus is built up around the otic vesicle. The otic vesicle, like the optic vesicle, is lined by an epithelium of epiblastic origin, but is not like that vesicle budded off from the medullary canal. It takes origin in an involution of the skin covering the head; for a time the epithelium of the vesicle is continuous with the epidermis of the skin, and wholly unconnected with the developing brain; later on the epithelial involution separates from the skin, becomes a closed independent vesicle, and makes connections with the brain through the auditory nerve growing out to meet it. The otic vesicle therefore is not like the optic vesicle a part of the brain, and we find accordingly the structure of the auditory epithelium much more simple than that of the retina; it corresponds only to a part of the retina, to the more external layers of the retina, not to all of them.

We have seen that the optic fibres are connected with a part only of the optic vesicle, with the anterior wall only of the retinal cup and not with the whole of this; the part of the anterior wall which forms the pars ciliaris retinæ and the whole of the posterior wall make no connections with the optic fibres and remain in the form of a relatively simple epithelium. The connection of the auditory nerve with the walls of the otic vesicle is still more partial; the nerve fibres become connected with the epithelium in a few limited areas. It is only in these areas that the epithelium lining the otic vesicle becomes differentiated into the special auditory epithelium; elsewhere it possesses relatively simple characters.

The cavity of the optic vesicle is, as we have seen, soon obliterated by the coming together of the anterior and posterior walls. The cavity of the otic vesicle is permanent, growing with the growth of the organ and becoming filled with a peculiar fluid secreted by the walls, called *endolymph*. The vesicle as it grows soon loses its early simple, more or less spherical form and assumes a most complicated shape, becoming divided into the parts known as the utricle with the semicircular canals, the saccule, and the canalis cochlearis; of these we shall speak in detail later on.

§ **809**. While the vesicle is assuming this complicated shape, the mesoblastic tissue investing it undergoes a differentiation. The tissue immediately in contact with the epithelium becomes connective tissue serving as a dermis to support the epithelium, so that the vesicle becomes a (complicated) sac with membranous walls lined with epithelium specially modified into auditory epithelium at particular places, at which places and at which places alone the auditory nerve makes connections with the walls.

The outer portion of the mesoblastic tissue is converted into bone of a somewhat dense character, and thus furnishes a bony shell or envelope enclosing and to a large extent following the contour of the complicated membranous sac. Between the outer bony envelope and the inner membranous sac is developed a large irregular lymphatic space which (Fig. 172) follows to a great extent the contour of the sac, but is broken up by broad adhesions of the membranous sac to the periosteum lining the bony envelope or by narrower bridles of connective tissue crossing the space; some of these form beds for the branches of the auditory nerve on their way to the auditory epithelium. The fluid in this space, which is lymph and which has access to the lymphatics of neighbouring parts, receives the special name of *perilymph.* A portion of the sac, with its surrounding perilymph space and bony envelope, undergoes a development differing materially from that

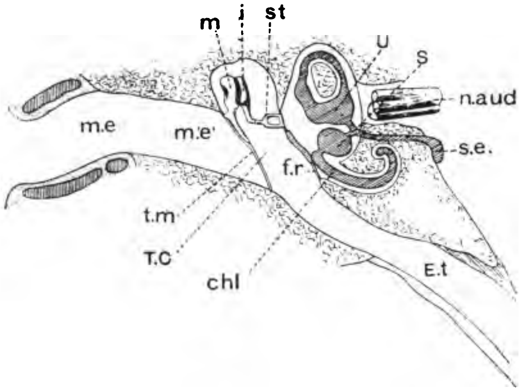

Fig. 172. Diagram to illustrate the general structure of the ear. (After Schwalbe.)

The figure is purely diagrammatic, intended only to shew in one view all the several important parts in relation to each other; such a view is in the actual ear impossible.

*m. e.* the external meatus or auditory passage, in the outer part where the walls are cartilaginous, *m'. e'.* the same in the inner part where the walls are osseous.

*T. C.* the tympanic cavity. *t. m.* the tympanic membrane. *m.* malleus, *i.* incus, *st.* stapes, attached to the fenestra ovalis. *f. r.* fenestra rotunda. *E. t.* Eustachian tube.

*U.* the utricle, with the perilymph space around. One semicircular canal with its ampulla is shewn, with the bony core of the hoop. *S.* Saccule. *s. e.* sacculus endolymphaticus lying within the cranial cavity, and connected by the ductus endolymphaticus with both saccule and utricle. *chl.* the canalis cochlearis, connected with the saccule by the canalis reuniens, and surrounded by its perilymph space, scala vestibuli, and scala tympani, the latter ending at the fenestra rotunda, the former continuous with the perilymph space of the vestibule around the utricle and saccule; the cochlea is shewn diagrammatically as a simple curve, the scala vestibuli and scala tympani being continuous at the top.

*n. aud.*, the auditory nerve, shewing the three main divisions of the trunk.

of the rest of the sac, and is known as the *cochlea.* The bony envelope surrounding the parts of the membranous sac known as the utricle and saccule does not follow closely the contour of those parts but remains as an undivided part called the *vestibule* (Fig. 173); the parts of the membranous sac called the semicircular canals are however followed somewhat closely by the bony envelope. The whole bony envelope may be dissected out from

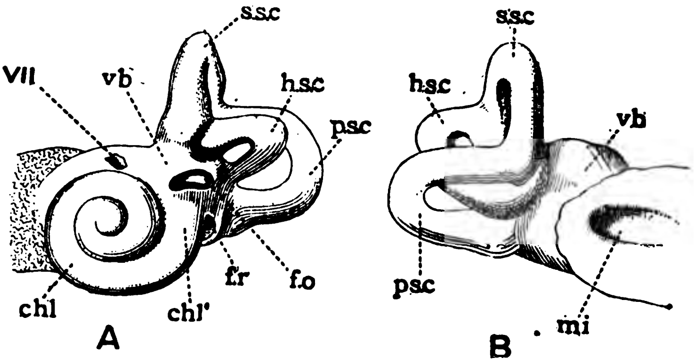

FIG. 173. THE BONY LABYRINTH. LEFT EAR. (Schwalbe.)

A. seen from the outside. B. seen from the median side. Both magnified twice. *Vb.* vestibule. *Chl.* cochlea. *Chl'.* the beginning of the first turn of the cochlea. *F.o.* fenestra ovalis, *f.r.* fenestra rotunda, *s.s.c.* superior, *p.s.c.* posterior, *h.s.c.* horizontal semicircular canals. *m.i.* meatus auditorius internus, canal for the auditory nerve. VII. opening of the canal containing the seventh nerve.

the spongy bone surrounding it, and may be obtained as a separate mass (Fig. 173), known by the name of the *labyrinth,* or *bony labyrinth* to distinguish it from the *membranous labyrinth* which lies within it, separated from it by the perilymph space. The bony labyrinth consists of cochlea, vestibule and semicircular canals, but the part of the membranous labyrinth corresponding to the vestibule is divided into utricle and saccule. The auditory nerve pierces the bony labyrinth at the so-called *meatus auditorius internus* (Fig. 173 *m. i.*) on its way to be distributed to the walls of the membranous sac.

All these structures, lying at first not far beneath the skin and forming together the 'internal ear,' as they grow come into close connection with a passage on the side of the head leading from the exterior into the pharynx and known as the "first" or "hyomandibular visceral cleft." By a series of changes, which we need not describe here, and indeed about which there is some divergence of opinion, this simple primitive passage is replaced in the adult by two passages separated from each other by a partition known as the *membrana tympani* (Fig. 172 *t. m.*) or tympanic membrane. On the outer side of the membrane lies a tubular channel, the *external auditory meatus* (*m. e., m.'e.'*), lined by skin, and opening on to the exterior by an orifice guarded with the "pinna" or "auricle." On the inner side of the membrane lies the drum-shaped *tympanic cavity* (*T. C.*), often called the "middle ear," which through the tubular *Eustachian tube* (*E. t.*) opens into the pharynx, and which is lined throughout by mucous membrane continuous with that of the pharynx.

The 'internal ear' forms the mesial side of the more or less flattened and drum-shaped tympanic cavity opposite to the outer side which is to a large extent formed by the tympanic membrane; and at two places the osseous tissue of the bony envelope of the internal ear is wanting, the gaps giving rise to what in the dried skull appear as two foramina, but in the fresh state are two membranous fenestræ. One of these, oval in shape, called the *fenestra ovalis* (Figs. 172, 176, 178 *f. o.*), lies between the tympanic cavity on the outside and that part of the perilymph space which surrounds the division of the membranous labyrinth known as the utricle on the inside; in the dried bony labyrinth (Fig. 173 *F.o.*) it appears as a hole in the vestibule. The other, round in shape, called the *fenestra rotunda* (Figs. 172, 176 *f. r.*), lies between the tympanic cavity and a part of the perilymph space which enters into the construction of the cochlea; as we shall see, the perilymph space of the cochlea may be regarded as a peculiar tubular prolongation of that of the vestibule, and the membrane of the fenestra rotunda closes as it were the end of this prolongation.

Certain bones of the skull, converted by striking developmental changes into a jointed chain of minute bones, *the auditory ossicles* (Fig. 172 *m. i. st.*), are by processes of growth thrust into the tympanic cavity in such a way that they eventually seem to lie wholly in the cavity, and to form a bridge across the cavity between the tympanic membrane on the outer side, and the fenestra ovalis on the mesial side. The ossicles are three in number; to the tympanic membrane is attached the *malleus*; this is joined to the *incus*, which in turn is joined to the *stapes*, the end of which is attached to the fenestra ovalis. Into the details of these ossicles we shall enter presently.

§ **810.** The affections of consciousness, which we call sensations of sound, are the result of auditory impulses reaching certain parts of the brain along the auditory nerve; and these auditory impulses are generated through vibrations, or rhythmically repeated variations of pressure, which we call 'waves of sound,' in some way or other acting upon the terminations of the auditory fibres in the auditory epithelium. The waves of sound gain access to the epithelium by means of the perilymph, passing probably in some parts directly through the dermis of the membranous sac to the overlying epithelium, and being in other parts transmitted to the endolymph from the perilymph across the membranous walls, and acting on the epithelium through the endolymph.

Waves of sound may be and to a certain extent are conducted in a direct manner to the perilymph, through the tissues, especially the harder bony tissues, of the head, reaching the perilymph across its bony envelope. The vast majority however of the waves of sound which fall upon the head travel through the medium of the air, and in order to reach the perilymph have to pass from a gaseous medium, the air, into the solid and liquid media of the head. Now the vibrations of particles constituting waves of sound are not readily communicated from a gaseous to a liquid or solid medium; special conditions are required to effect this. The transference of sound from the air to the perilymph is attended with considerable difficulty; and the parts of the ear which we have spoken of above as constituting the middle and outer ear, serve as an acoustic apparatus for facilitating this transference and thus bringing the aerial waves to act on the auditory epithelium; the action of the apparatus being somewhat as follows.

Waves of sound falling on the side of the head reach the tympanic membrane by the external meatus, and throw that membrane into vibrations. These vibrations are transmitted through the chain of ossicles to the membrane of the fenestra ovalis and so to the perilymph lying on its far side; sweeping over the perilymph in its continuous cavity the waves eventually break upon the fenestra rotunda, having on their way affected the auditory epithelium. We have first to inquire how this subsidiary acoustic apparatus performs its work.

### *The Conducting Apparatus of the Tympanum.*

§ **811.** *The auditory ossicles.* The *malleus*, or hammer bone (Fig. 174 A and D), has a rounded head (*cp.*) bearing a peculiar saddle-shaped surface for articulation with the incus, and ends below in a tapering process, the *manubrium*, or handle (*mbr.*) by which it is attached, in a manner to be described presently, to the inner surface of the tympanic membrane. To the handle at its upper part is attached on the inner side the tendon of the tensor tympani muscle (Figs. 177, 180, 183 *T.T.*); and at the top of the handle, on the outer side, is a short blunt process, *processus brevis* (Fig. 174 A *p.b.*), which as we shall see abuts on a particular part of the tympanic membrane. Still higher up is a thinner and generally much longer process (Fig. 174 A *p.f.* and Fig. 183 *p.f.*), *processus gracilis* or *Folianus*, the base of which with part of the thick neck of the malleus above serves for the attachment of ligaments, and the end of which is inserted into a fissure in the bony wall of the cavity.

The *incus*, *ambos*, or anvil bone (Fig. 174 B and D) has a less well-defined head, bearing a surface for the articulation with the malleus, and a short body which immediately divides into two processes at right angles to each other. One of these, the "short process" (*p′. b′.*), takes up a horizontal position (Fig. 183 *p′. b′.*) and is attached to the wall of the tympanum by a ligament (Fig. 181 *lg. inc.*). The other "long process" (Figs. 174, 180, 183 *p′. l′.*) or 'shaft,' tapering and somewhat curved, takes up a vertical position parallel to the handle of the malleus, but at its end makes a sudden bend mesially towards the internal ear (Fig. 172) and terminates in a flattened knob, with which it is articulated to the stapes (Fig. 174 D). This knob, having frequently at least an independent ossification, is sometimes spoken of as the *os orbiculare* or *lenticulare.*

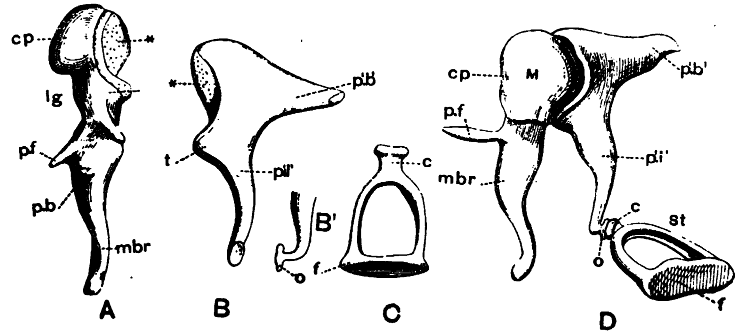

Fig. 174. The Auditory Ossicles. (After Schwalbe and Helmholtz.) Magnified four times.

A. *The malleus.* *cp.* the head (caput). *the articulating surface for the incus, *t.* Tooth locking with tooth of incus. *lg.* is placed opposite the attachment of the ligaments. *p. f.* processus gracilis or Folianus, represented as short. *p. b.* processus brevis. *m. br.* handle (manubrium).

B. *The incus.* *surface articulating with malleus. *t.* tooth locking with tooth of malleus. *p′. b′.* processus brevis. *p′. l′.* processus longus.

B′. The lower end of the processus longus seen sideway; *o*, its expanded termination or os orbiculare.

C. *The stapes.* *c.* the head. *f.* the foot-plate.

D. The three ossicles in connection. *M.* malleus, *I*, incus, *st.* stapes; the other letters as above.

The *stapes* or stirrup bone (Fig. 174 C and D), which is placed horizontally at right angles to the shaft of the incus, consists of a head (*c*) articulating with the extremity of the shaft of the incus, and an oval foot-plate (*f*), attached, in a manner which we shall presently describe, to the fenestra ovalis, the two being united by curved limbs after the fashion of a stirrup.

§ **812**. The tympanum, in which these ossicles lie, may be compared to a low drum placed obliquely at the end of the external meatus. The outer lateral side or surface of the drum is furnished by the tympanic membrane, the inner mesial side or surface by the bony labyrinth; but the two sides are not exactly parallel, and the mesial side is much broken up by irregularities. The cavity of the drum is not completely circumscribed by a circular

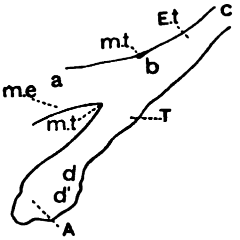

FIG. 175. DIAGRAM TO ILLUSTRATE THE RELATIONS OF AUDITORY PASSAGE, TYMPANUM, AND EUSTACHIAN TUBE. (After Schwalbe.)

**The figure represents a section not quite horizontal, being inclined downwards in front; the right-hand edge of the page may be taken to represent the median plane of the head.**

***m. e.* external meatus, *T.* the tympanic cavity. *E. t.* the Eustachian tube. *A.* is placed in the antrum mastoideum. *m. t.* indicates the attachment of the tympanic membrane.**

***a, b,* the axis of the external meatus, *c. b. d.* that of the Eustachian tube. *d d'.* shews the curved axis of the antrum.**

wall like that of a drum proper. In about the lower half of the cavity (Figs. 176, 177) the wall though irregular is complete; but the upper half of the cavity is continuous along an axis oblique to the axis of the meatus (Fig. 175) with two more or less tubular cavities, one stretching upwards and backwards (Fig. 175 *d d.'*), the other downwards and forwards (Figs. 175, 176, 177 *E. t.*). The latter, distinctly tubular, is the Eustachian tube leading from

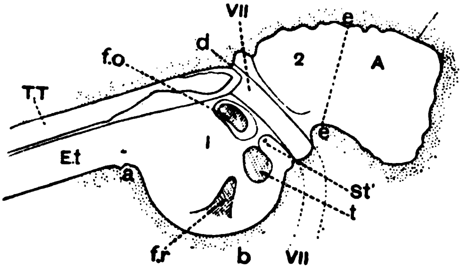

FIG. 176. DIAGRAM OF THE MEDIAN WALL OF THE TYMPANUM OF THE LEFT EAR. Magnified twice. (After Schwalbe.)

**1. The tympanic, 2. the epitympanic region; below the reference figure is seen the gentle prominence due to the ampullæ. *A*, the antrum mastoideum, the line *ee* marking its limits. *E. t.* the Eustachian tube. *T. T.* the groove for the tensor tympani. *f. o.* the depression of the fenestra ovalis, the fenestra itself being shaded. *f. r.* the depression leading to the fenestra rotunda; above, and obliquely to the left of this, lies the projection caused by the base of the cochlea. *St.* the prominence for the stapedius, with the orifice for the exit of the tendon. VII, the course of the facial nerve. The tympanum proper lies within the letters *a. b. d. e.***

the upper front part of the tympanum obliquely forwards, downwards and towards the median plane of the head into the pharynx. The former continues the upper hind part of the tympanum upwards, backwards and away from the median line of the head, first as an irregular space, sometimes called the "epitympanic region," and then farther backwards as a larger space, the *antrum mastoideum* (Fig. 176 A), which in turn communicates with the labyrinth of spaces or "air cells" of the mastoid bone.

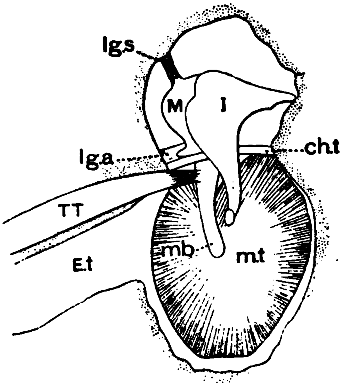

Fig. 177. Diagram of the outer wall of the Tympanum (Right Ear) as seen from the mesial side. Magnified twice. (After Schwalbe.)

*m.t.* membrana tympani. *mb.* handle of *M* the malleus. *I.* the incus. *E. t.* Eustachian tube. *T. T.* tensor tympani, the tendon of which is seen attached to the upper part of the handle of the malleus. *lg. a.* the anterior and *lg. s.* the superior ligament of the malleus. *ch. t.* the chorda tympani nerve traversing the tympanic cavity.

The ossicles are placed more or less vertically but yet obliquely in the tympanic cavity in such a way that the heads and bodies of the malleus and incus lie above the tympanum proper in the epitympanic region (Fig. 177), but the handle of the malleus and the shaft of the incus descend to the centre of the tympanum. Opposite but rather above this centre is seen in the median wall of the tympanum a funnel-shaped depression (Figs. 176, 178 *f. o.*) at the bottom of which lies the fenestra ovalis; and to this the stapes, horizontal but slightly inclined upwards, passes from the end of the shaft of the incus.

In the lower part of the median wall, some distance below the fenestra ovalis, is seen an irregular depression (Fig. 176 *f.r.*) which leads to the fenestra rotunda; and by the side and above this, occupying the central portion of the median wall of the tympanum proper, is a projection marking the position of the first whorl or base of the cochlea. The fenestra ovalis itself marks the position of the junction of the utricle and saccule, and in the epitympanic region, above a rounded ridge caused by the projection of the Fallopian canal carrying the seventh or facial nerve (Fig. 176 VII.) is a protuberance marking the position of the swollen ends or ampullæ of two of the semicircular canals, namely those known as the horizontal and superior.

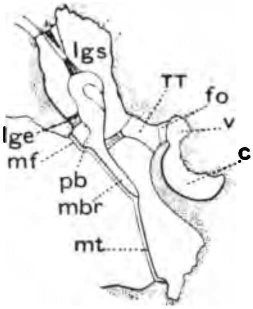

Fig. 178. Frontal (transverse vertical) section through the Tympanum. (Left Ear.) (Schwalbe.)

The figure, partly diagrammatic, is magnified twice, and shews the front part of the tympanum as seen from behind; the incus has been removed, the articular surface on the head of the malleus being indicated.

*mt.* The membrana tympani. *mf.* membrana flaccida. *mbr.* handle of the malleus. *p. b.* short process of the malleus.

*lg. e.* external ligament, *lg. s.* the superior ligament of the malleus.

*TT.* The bony projection from which the tendon of the tensor tympani passes to the malleus. *f. o.* the fenestra ovalis. *v.* the front part of the vestibule. *c.* the beginning of the first (basal) turn of the cochlea.

The distance across the tympanum between the beginning of the chain of ossicles at the point of the handle of the malleus and its end at the fenestra ovalis is very short, much shorter than the length of the chain itself; the greater part of the chain, including the bodies and processes of, that is to say nearly the whole of, the malleus and incus, owing to the peculiar form and articulation of the ossicles, lies above a line drawn from the point of the handle of the malleus to the fenestra ovalis. Cf. Figs. 177, 178. We must now turn to the details of the manner in which the ossicles are attached to the membrana tympani, to each other, and to the fenestra ovalis.

§ **813**. The *membrana tympani* (Fig. 179) irregularly elliptical in form with the long axis vertical is placed obliquely (Figs. 172, 178 *m. t.*), at the inner end of the external meatus. Nearly the whole of the circumference of the membrane is fixed in a groove of the ring-shaped bone, the annulus tympanicus. At the extreme top the ring is wanting; and the portion of the membrane thus attached, not to the ring but to the bone above, being less tense than the rest of the membrane, and indeed thrown into folds, is distinguished as the *membrana flaccida*

(Fig. 179 *m. f.*). The short process of the malleus abuts against this part of the membrane (Fig. 178 *p. b.*), and when the membrane is viewed from the outside, as in looking down the meatus, is seen shining through it (Fig. 179 *p. b.*).

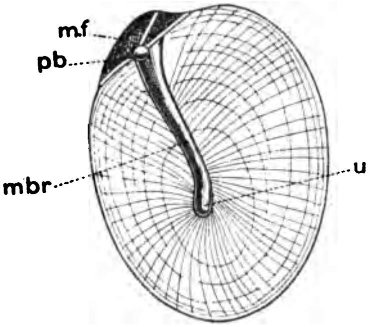

Fig. 179. The Membrana Tympani. (After Schwalbe.) (Magnified four times.)
The membrane is seen from the external meatus and the handle of the malleus, *mbr*, is represented as shining through. *m. f.* the membrana flaccida, the folds of which are represented radiating from *p. b.*, the projection outwards caused by the end of the short process of the malleus. *u.* the umbo of the membrane, to which is attached the end of the handle of the malleus. The figure shews diagrammatically, the radial and circular fibres of the membrane.

This larger tenser part of the membrane forms a shallow funnel, the apex of which. called the *umbo* (Fig. 179, 180 *u*), projects into the tympanic cavity; and the handle of the malleus is attached to this part of the membrane on its inner side in such a way that the umbo is supported by the tip of the handle. The umbo is somewhat eccentric in position, lying nearer the bottom than the top; and the sides of the funnel are not flat, but slightly convex towards the meatus, though not equally so in all parts.

The membrane consists of a basis of connective tissue, *membrana propria*, covered on the outside by a continuation of the skin of the meatus, and on the inside by the mucous membrane lining the tympanum. The connective tissue basis, which is absent from the small flaccid part of the membrane, consists of bundles of connective tissue, somewhat peculiar in appearance, but yet ordinary, fibrillated, inelastic, gelatiniferous connective tissue, arranged in an outer layer of radiating bundles, and a thinner less complete inner layer of circularly disposed bundles; both layers, especially the circular, are thinner towards the centre than at the circumference. The handle of the malleus is imbedded in, and wrapped round by the bundles of this connective tissue, the radial bundles radiating from the umbo, or in the upper part of the membrane diverging by the sides of the handle.

The skin covering the outer side of the membrane is ordinary skin consisting of dermis and a rather thin epidermis, in which the distinction between the malpighian and corneous layers is not very sharp. Blood vessels and a nerve (nervus membranæ tympani, a branch of the auriculo-temporal) run in the dermis. The mucous membrane, lining the inner surface of the membrane, consists of a single layer of flattened non-ciliated epithelium cells lying on a dermis in which is much reticular connective tissue. It will be understood that this mucous membrane is continued over the handle of the malleus, as indeed over the rest of the ossicles.

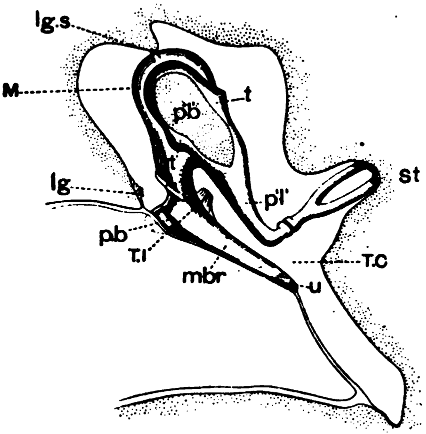

FIG. 180. THE OSSICLES IN POSITION. Magnified four times. (After Hensen.)

The figure represents a section through tympanum in the line of the long axis of the malleus and incus; the short process of the incus *p'b'* has been cut through.

*T.C.* The tympanic cavity. *mbr.* handle of malleus. *u.* umbo. *p.b.* short process of the malleus shewn in dotted outline as pushing outwards the membrana flaccida. *T.I.* the attachment of the tendon of the tensor tympani. *lg.* the attachment of the external ligament of the malleus. *lg.s.* the superior ligament of the malleus. *t.t.* the teeth of the incus. *p'l'.* the long process, shaft, of the incus. *St.* the stapes.

§ **814.** The handle of the malleus being thus firmly imbedded in the substance of the tympanic membrane moves with every movement of it; the attachment of the short process to the flaccid part of the membrane is of a looser character. Besides this attachment to the tympanic membrane the malleus is further bound to the wall of the tympanum by three ligaments of connective tissue. One, the superior ligament (Figs. 177, 178, 180 *lg.s.*), descends from the upper wall of the tympanum to the head of the malleus, whose movements it thus steadies. More important however than this are the other two ligaments which pass more or less horizontally from the outer wall of the tympanum above the tympanic membrane, to the neck of the malleus. One placed anteriorly (Figs. 177, 181 *lg.a.*), the anterior ligament, embraces the long or Folian process, the other, the exterior ligament

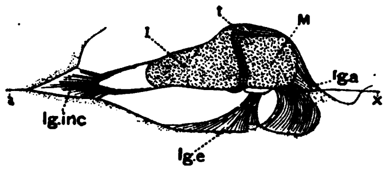

Fig. 181. The Ligaments of the Ossicles. (After Hensen.)

The figure represents a nearly horizontal section of the tympanum, carried through the heads of the malleus and incus.

*M.* malleus. *I.* incus. *t.* articular tooth of incus. *lg. a.* anterior and *lg.e.* external ligament of the malleus. *lg.inc.* ligament of the incus.

The line *ax* represents the axis of rotation of the two ossicles.

(Fig. 181 *lg.e.*), is placed more externally; the two are nearly continuous, leaving however a distinct gap (Fig. 181) between them. They serve to limit the movements of and so to keep in place the head of the malleus, which it is said still remains in position even after the incus has been removed.

The joint between the malleus and incus, which like other joints has articular cartilages, synovial membrane, a capsule and ligaments, the latter being very slender, is of a peculiar shape, the lower part of the articular surface of each bone projecting in the form of blunt teeth (Figs. 174, 180, 181, 183 *t.*). These teeth lock into each other in such a way that when by an inward movement of the tympanic membrane the malleus is carried inwards, the incus is necessarily carried inwards also, but that when the malleus is moved outwards, that is towards the external passage, the incus does not necessarily follow it. Hence while every inward movement of the tympanic membrane leads to an inward movement of the malleus, incus and stapes, in succession, the three falling back into their previous positions when the movement ceases, should the tympanic membrane for any reason be pushed unduly outwards into the meatus, the joint between the malleus and incus gapes and so prevents the stapes being pulled out of the fenestra ovalis.

A ligament, ligament of the incus (Fig. 181 *lg. inc.*), more or less divisible into two parts, passing from the median wall of the tympanum to the end of the short process of the incus, firmly secures that part of the chain of ossicles. The long process of the incus hangs nearly vertically downwards but its end turning sharply round at right angles expands into a flattened knob, which, covered with cartilages, forms a joint with the cartilage covered head of the stapes (Figs. 174 B′ and D, 182).

The foot of the stapes (Fig. 182), an irregularly oval plate of bone, covered on the side towards the internal ear with cartilage, has its long diameter, about 3mm., placed horizontally, the vertical diameter being about 1·5 mm. It corresponds in form, but is rather smaller than the fenestra, and between its cartilaginous rim and the cartilage-lined rim of the fenestra is attached a ring-shaped membrane (Fig. 182, 6), consisting of radially disposed bundles of connective tissue with which many elastic fibres are mixed. The ring, though slightly broader in the front part than in the hind part of the oval, is very narrow, at most 100 $\mu$; hence the movements of the stapes within the fenestra are very limited in extent, and probably do not exceed a small fraction ($\frac{1}{81}$ to $\frac{1}{14}$) of a millimeter. The tympanic surface of the fenestra and included stapes is covered with a continuation of the mucous membrane which covers the tympanic membrane, and which not only lines the whole tympanic cavity but is also reflected over the whole chain of ossicles; the other surface of the stapes, that which forms part of the perilymph space of the labyrinth, is lined like the rest of the cavity with a lymphatic epithelium.

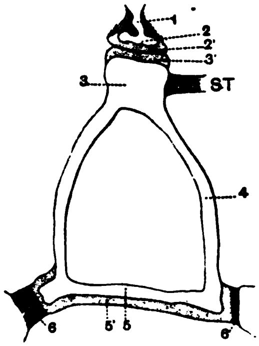

FIG. 182. THE STAPES IN POSITION. Much magnified. (Schwalbe.)

1. The end of the shaft of the incus. 2. Its expansion or os orbiculare. 2'. The articular cartilage of the same. 3. The capitulum of the stapes. 3'. Its articular cartilage. 4. The hoops of the stapes. 5. The foot-plate of the stapes. 5'. Its articular cartilage. 6. The membrane of the fenestra ovalis.

*ST*. The tendon of the stapedius muscle attached to the capitulum of the stages.

§ **815**. The chain of ossicles, thus jointed together, attached to the tympanic membrane at one end, and to the fenestra ovalis at the other, and secured by ligaments, may be regarded as a lever. Observations and experiments shew that the end of the short process of the incus serves as the fulcrum, the power being applied at the umbo in which the handle of the malleus ends, and the effect being brought to bear on the end of the long process of the incus attached to the stapes. In thus acting as a lever the heads of the malleus and incus rotate round a horizontal line drawn through them in the direction of the line *ax* in Fig. 181. Such a lever may be represented by the line *xx'* in Fig. 183.

Careful measurements shew that the whole length of the line from *F* the fulcrum to *P*, where the power is applied, is about 9·5 mm., while the length from *F* to *W*, where the effect is brought to bear, is about 6·3 mm. Hence when the tympanic membrane is driven inwards, the corresponding inward movement of the stapes in the fenestra is as far as extent is concerned only about two-thirds of that of the tympanic membrane. By the principle of the lever however the amount of pressure exerted by the movement of the stapes, the force of the movement is one and a half times greater than the force expended in producing the movement of the tympanic membrane. The arrangement of the lever of ossicles therefore is such as to convert a relatively large movement into a smaller movement of greater intensity; the benefit of such a conversion is obvious.

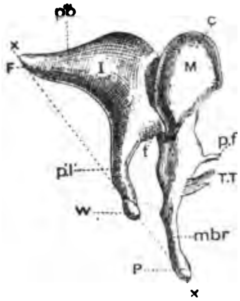

**Fig. 183. The Malleus and Incus, in position. (Helmholtz.)**

**M.** The malleus. *c*, the head, *mbr*, the handle, *p.f*, processus Folianus. *T.T.* the tendon of the tensor tympani.

**I.** The incus. *p'b'*, the short process, *p'l'*, the long process, *t*. tooth locking with the malleus.

The line *XX* represents the lever formed by the two ossicles, with, *F*, the fulcrum at the attachment of the short process of the incus, *P*, the point where the power is applied at the end of the handle of the malleus, *W*, the point where the effect is produced at the os orbiculare of the incus.

### *The Conduction of Sound through the Tympanum.*

§ **816.** The conduction of sound from the external air to the labyrinth takes place by means of the tympanic membrane and the chain of ossicles acting as a lever in the manner just described.

Stretched membranes have the property of being readily thrown into vibrations by aerial waves of sound, and of transmitting the vibrations to bodies in contact with themselves. The tympanic membrane is a stretched membrane which, by its size, nature and conformation is specially adapted to take up and transmit a great variety of vibrations. Sound is a vibration of the particles of matter, a series of movements of the particles from and to a fixed point. In air and other gases the movements of the particles lead to alternating condensation and rarefaction of the medium, the sound is propagated as waves of alternating condensation and rarefaction, which since the to-and-fro movement of the particles is in the same direction as that in which the undulations are travelling, are spoken of as 'longitudinal' waves. In liquids the transmission of sound also takes place by longitudinal waves of alternating condensation and rarefaction, and sound may travel through solids in the same way. But solids in the form of membranes or plates, strings, and rods may also give rise to sounds by being thrown into bodily vibrations, a rod for instance bending alternately to-and-fro in rapid succession. In such a case the particles of the rod move sensibly in a direction transverse to the long axis of the rod; and the vibrations of this kind, thus giving rise to sounds, are spoken of as "transversal" vibrations. It will be understood that a rod, membrane, plate or string, may also be the subject of longitudinal vibrations; but the sound given out by such longitudinal vibrations differs from that given out by transversal vibrations of the same body. A rod, string, or membrane thrown into sufficiently rapid and strong transversal vibrations will communicate its vibrations to the surrounding air, and so give forth a sound, which will travel through the air in the form of waves of longitudinal vibrations. Conversely, sound travelling through the air in waves of longitudinal vibrations, and striking upon a rod, string, or membrane, may throw it into transversal vibrations. And this is what takes place in the ear. Aërial waves of sound, in the form of longitudinal vibrations, alternating condensations and rarefactions, of the air, travelling along the meatus, fall upon the tympanic membrane, and throw it into transversal vibrations; the membrane bends bodily inwards and outwards in time with the condensations and rarefactions of the air in the meatus on its outer surface.

The vibrations of a rod, a tuning-fork for example, are comparatively simple in character; and we find, correspondingly, that a tuning-fork is very limited in its power of 'taking up' sounds from the air, of being thrown into vibrations by sounds falling upon it; it will only take up from the air the particular sounds, the particular tones as we shall presently call them, which it itself gives forth when thrown into vibrations by being struck. The vibrations of a membrane are much more complex; and for this reason a membrane takes up much more readily a variety of different sounds reaching it through the air. Still every membrane has its fundamental tone or tones, as they are called, those which it naturally gives forth when thrown into vibrations; and it takes up these from the air much more readily than any other sounds. It is a feature of the tympanic membrane that it takes up, without any marked distinction, a very great variety of sounds within a very large range. It probably has a fundamental tone of its own, but this is kept in the background; it is not prominent, and does not materially influence our hearing. Were it otherwise, were the tympanic membrane thrown into vibration much more readily by a particular sound than by any others, that sound would be dominant in all our hearing; and unless, as in vision, psychical experience intervened to correct the mere sensation, we should be misled in our judgments as to what was taking place around us.

This general usefulness of the tympanic membrane is secured partly by features proper to itself, partly by the fact that it is 'damped' by the attachment to it of the chain of ossicles. Without attempting to enter into a discussion of a matter which is in many ways complex, we may say that the following features contribute to make the tympanic membrane sensitive to a large variety of sounds. In the first place, its dimensions are relatively small. In the second place, the material of which it is composed is peculiar, so that it is in a special way unyielding and rigid; it retains its form when cut away from its bony attachments by a circular incision, and the malleus, including its handle, may be removed from it without distorting it. In the third place, its remarkable form, that of a shallow funnel with sides gently convex towards the meatus, has a marked effect upon its capabilities of vibration. The chain of ossicles, attached at its far end, to the membrane of the fenestra ovalis has a 'damping' effect, similar to that, familiar to every one, of lessening or stopping the sound of a vibrating empty wine-glass or tumbler by pressing the finger on it; and this 'damping' while it diminishes to a certain extent all the vibrations of the membrane is especially effective in the case of excessive vibrations, such as those which might be produced by the sound which is the fundamental note of the membrane.

§ **817.** The vibrations thus set going in the tympanic membrane are transmitted from it to the chain of ossicles. The transmission might take place in two ways. In the first place, the vibrations, the alternate bendings inwards and outwards of the membrane, might, by carrying with it the attached handle of the malleus, work the chain of ossicles as a lever, in the manner described in § 815, so that each inward flexion of the tympanic membrane led to the membrane of the fenestra ovalis pushing the perilymph of the labyrinth inwards, while the return outwards again of the one led to a like return of the other. In the second place, the transversal vibrations of the tympanic membrane might set up longitudinal vibrations in the substance of the malleus, which would travel as longitudinal vibrations through the chain, and so reach the perilymph. In the one case the whole chain of ossicles swings to and fro, in the other case the sound is propagated by molecular movement. That the ossicles do move *en masse* has been proved by recording their movements in the usual graphic method. A very light style attached to the end of the incus or to the stapes is made to write on a travelling surface; when the tympanic membrane is thrown into vibrations by a sound, the curves described by the style indicate that the chain of bones moves with every vibration of the membrane. On the other hand, the comparatively loose attachments of the several ossicles is an obstacle to the molecular transmission of sonorous vibrations through them. Moreover, sonorous vibrations can only be transmitted to or pass along such bodies as either are very long compared to the length of the sound-waves, or, as in the case of membranes and strings, have one dimension very much smaller than the others. Now the bones in question are not only not especially thin in any one dimension, but are in all their dimensions exceedingly small compared with the wave-lengths of the vibrations of even the shrillest sounds we are capable of hearing; hence they must be useless for the molecular propagation of vibrations. We may conclude then that when waves of sound throw the tympanic membrane into vibrations, each inward excursion of the membrane is followed by a corresponding impulse given by the foot of the stapes to the perilymph. As we have seen, the space through which the end of the incus moves is less than that through which the handle of the malleus moves, and the movements of the stapes are in addition restricted by the manner of its attachment to the rim of the fenestra ovalis; but the energy with which the end of the incus, and hence the stapes, moves is proportionately increased, so that we might almost speak of the gentle swingings of the tympanic membrane being converted into smart taps on the perilymph of the labyrinth.

The impulses thus given to the perilymph at the fenestra ovalis travel along the intricate passages of the perilymph spaces, the details of which we shall presently study, and finally break upon the fenestra rotunda; if the membrane which closes this orifice be watched it may be observed to pulsate in sequence with the pulsations of the fenestra ovalis. During their passage these impulses are communicated to the endolymph and in some way or other affect the endings of the auditory nerve. How they do this we shall presently study; but we may here call attention to the fact that the waves of sound which fall on the tympanic membrane are for the most part not simple in character but complex, and in many cases exceedingly so. This complexity is carried on into the vibrations of the tympanic membrane and so into the impulses given to the perilymph; the waves which sweep past the endings of the auditory nerve are, so to speak, reproductions of the complex aërial waves passing down the meatus.

§ **818.** By far the greater number of the sounds which we hear reach the tympanic membrane by passing through the air down the meatus. One great use of the long external passage is probably to protect the delicate tympanic membrane from the accidents to which it would be subject were it freely exposed on the surface of the body; but it has also a use in transmitting to the tympanic membrane sounds travelling to the ear in certain directions more readily than those coming in other directions. The constriction of the meatus at the junction of the outer and middle third serves as a sort of diaphragm by which waves of sound travelling too much out of the line of the meatus are turned back. The external ear, auricle, or pinna has also probably a similar effect, reflecting into the meatus waves which fall upon it in a particular direction or waves of a particular kind. But of these uses, which are of more importance in some animals than in man, we shall speak again in considering the manner in which we recognize the directions of sounds.

Sounds, however, may reach the ear by paths other than the meatus. If a tuning-fork be struck and then held near the ear it will after a while cease to be heard, the sound dies away; but the sound is heard again if the handle of the fork be placed between the teeth; and when the sound again dies away, it may be revived by gently closing the external meatus, care being taken not to cause compression of the air within. When the tuning-fork is held between the teeth its vibrations are transmitted, through the bones of the head to the tympanic membrane, which thus set in motion acts in the same way as when it is set in motion through the air of the meatus. That the vibrations which thus reach the internal ear are, for the most part at least, conducted through the tympanum, and not brought to bear on the perilymph directly through the bony walls of the labyrinth, is not only indicated by the effect just mentioned of closing the meatus, for this could have no influence on the labyrinth itself, but may be also proved by experiment. If a style be attached to the stapes laid bare in the skull, the vibrations of a tuning-fork brought into contact with the skull will lead to corresponding movements of the style.

Not only may vibrations be transmitted from the skull to the tympanic membrane, but also conversely the vibrations of the membrane, brought about in the usual way through the meatus, may be transmitted to the bones of the skull. If a long tube introduced into one meatus be spoken or sung into, the sounds may be heard by help of a stethoscope placed over various parts of the head. They are heard best perhaps at the opposite meatus; the vibrations of the bones of the skull set going by one tympanic membrane throw the other tympanic membrane also into vibrations.

§ **819.** Two muscles act upon the auditory apparatus of the tympanum; one, the *tensor tympani,* acts upon the malleus and hence upon the tympanic membrane, the other, the *stapedius,* acts upon the stapes.

The tensor tympani (Fig. 184) is a slender muscle, lying in a groove above the bony canal of the Eustachian tube, and having very much the direction of that tube. The tendon in which it ends, turns round, almost at right angles to the line of the muscle, over a bony prominence at the end of the groove, and passing athwart the cavity of the tympanum from the median side outwards (Fig. 178 *TT.*) is attached to the upper part of the handle of the malleus.

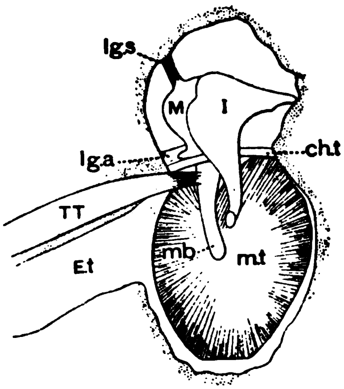

FIG. 184. DIAGRAM OF THE OUTER WALL OF THE TYMPANUM AS SEEN FROM THE MESIAL SIDE. Magnified twice. (After Schwalbe.)

*m.t.* membrana tympani. *mb.* handle of *M* the malleus. *I.* the incus. *E.t.* Eustachian tube. *TT.* tensor tympani, the tendon of which is seen attached to the upper part of the handle of the malleus. *lg. a.* the anterior and *lg. s.* the superior ligament of the malleus. *ch.t.* the chorda tympani nerve traversing the tympanic cavity.

The effect of the contraction of the muscle is to pull the handle of the malleus and so the tympanic membrane inwards towards the median side. Even in a quiescent state it may be of use in keeping up a certain amount of tension and in preventing the tympanic membrane being pushed out too far. When it contracts it certainly renders the tympanic membrane more tense; hence it has been supposed on the one hand to act as a damper lessening the amount of vibration of the membrane in the case of too powerful sounds, and on the other hand to accommodate the apparatus to the sounds falling upon it since the more tense membrane is more readily thrown into vibrations by higher notes and is less sensitive to lower notes. It has been urged that it is readily thrown into contraction at the commencement of a sound, especially of a noise, and returns to rest during the continuance of a prolonged musical note, the contraction being a simple contraction or twitch, rather than a continued tetanic contraction; it is suggested that this may serve to tune the membrane as it were for the sound which follows. Efferent impulses reach it through fibres of the fifth nerve which traverse the otic ganglion, and its activity is regulated by reflex action, vibrations of the tympanic membrane starting the afferent impulses. In some persons the muscle seems to be partly under the dominion of the will, since a peculiar crackling noise which these persons can produce at pleasure appears to be caused by contraction of the tensor tympani.

The stapedius is a small muscle imbedded in the bone of the median wall of the tympanum, the tendon issuing by a hole close to the fenestra ovalis (Fig. 176 *St.*) and being inserted into the head of the stapes (Fig. 182 *ST*). It is supposed to regulate the movements of the stapes, and especially to prevent the foot plate being driven too far into the fenestra ovalis during large or sudden movements of the tympanic membrane. Contractions of the muscle pull the front part of the stapedial foot plate towards the tympanum, the hind part being thereby pressed somewhat into the labyrinth and the whole membranous ring round the foot being rendered more tense; but the total effect is to diminish the pressure in the labyrinth. It perhaps may be regarded as the antagonist of the tensor tympani. It is governed by fibres from the facial nerve.

§ **820.** The cavity of the tympanum is, as we have seen, continuous with the Eustachian tube. The walls of the tube in the first third of its length adjoining the tympanum are osseous, but in the remaining two-thirds are cartilaginous and membranous. The tube, whose lumen is of varying diameter and special shape, passes obliquely forwards, downwards, and towards the median line (Figs. 176, 177 *E.t.*) to open at the side of the upper part of the pharynx. The mucous membrane lining the tube consists of a ciliated epithelium resting on a dermis rich in reticular and adenoid tissue, and bearing glands. The action of the cilia is such that the movement which they effect is directed from the tympanum to the pharynx. The mucous membrane lining the tympanum is a continuation of that lining the tube, and, like that, ciliated except over the tympanic membrane, the chain of ossicles, and probably some other parts; in these situations the epithelium consists of a single layer of flat non-ciliated cells, and a similar epithelium lines the antrum and mastoid cells which continue the cavity of the tympanum backwards and upwards.

One use of the Eustachian tube is to carry down to the pharynx the fluid, normally very small in amount, which is secreted by the mucous lining of the tympanum, but a far more important use is that of placing the air in the tympanum in communication with that in the pharynx, and so with the external air, by which means the pressure on the two sides of the tympanic membrane is equalized. If as sometimes happens the tube is definitely closed, the absorption of the gases in the air at first present in the tympanum diminishes the pressure on the inner side of the tympanic membrane, and so interferes with the vibrations of the membrane. Moreover it is desirable that general changes of pressure in the external atmosphere should be rapidly followed by corresponding changes in the pressure within the tympanum, since the tympanic membrane would not vibrate normally if any marked difference of pressure on the two sides were brought about; and this would result if the way from the tympanum to the external air through the tube were blocked.

The lumen of the tube has in its lower part the form of an obliquely vertical slit, the sides touching or nearly so; and much dispute has taken place as to whether the tube is normally closed or open. It is undoubtedly opened during the act of swallowing, and during the act, by the action of certain muscles of the palate, air is forced up into the tympanum. It may be opened also by a forced inspiration or a forced expiration when the nose and mouth are kept closed; in the former case the pressure of the air in the tympanum is diminished, in the latter case increased. Although under normal circumstances the lumen is so far patent as to allow the escape of the fluid driven by the cilia, the evidence goes to shew that it is practically closed; sounds for instance generated in the pharynx do not throw the tympanic membrane into vibrations in such a way as they would do if the tube were thoroughly open. Apparently the occasional opening, such as that effected by swallowing, is sufficient to keep the pressure within the tympanum at its proper level. When the general pressure of the external atmosphere is rapidly increased or diminished, temporary deafness, especially to low notes, frequently ensues, in consequence of the pressure within the tympanum not following the changes of the pressure without. This, however, is soon remedied by the act of swallowing, which opens the tube and thus equalises the pressure.

An abnormal permanency in the closure of the tube is recognized as a cause of deafness, and may be remedied by catheterism of the tube, that is to say, opening up the tube by passing an instrument into it from the pharynx.

## SEC. 2. THE STRUCTURE OF THE LABYRINTH.

**§ 821.** The membranous labyrinth, into which the primitive otic vesicle is developed, though very complicated in form, is virtually a sac the cavity of which filled with endolymph is continuous throughout. We may in the first place consider it as consisting of two divisions, which differ from each other both as to

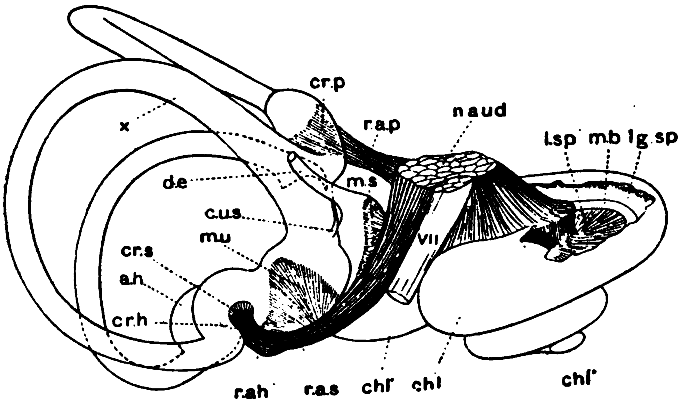

FIG. 185. THE MEMBRANOUS LABYRINTH (OF THE RIGHT EAR) AS SEEN FROM ABOVE, MAGNIFIED SIX TIMES. (After Retzius.)

**The bony envelope has been wholly removed from the vestibular division, but only in part broken through in the cochlear division.**

***chl.*** **the cochlea, *chl'* the first part of the basal whorl, *chl"*, the summit. To the right, where the bony wall has been broken through, are seen: *l.sp.* the spiral lamina, *m.b.* the basilar membrane, *lg.sp.* the spiral ligament.**

***n. aud.*** **the auditory nerve, lying alongside of which is seen VII, the seventh, facial nerve.**

***m.s.*** **macula of the saccule. *m.u.* macula of the utricle. *cr.p.* the crista of the posterior semicircular canal, with *r.a.p.* the branch of the auditory nerve distributed to it, *cr.s.* crista of the superior canal with *r.a.s.* its nerve. *a.h.* ampulla and *cr.h.* crista of the horizontal canal, with *r.ah.* its nerve.**

***x.*** **the conjoined posterior and superior canals. *d.e.* ductus endolymphaticus, with *c.u.s.* its junction with the utricle.**

their relations to the perilymph space and as to the manner in which the auditory nerve ends in them. One division is that part of the sac which enters into the construction of the cochlea, and is called the *canalis cochlearis* (Fig. 186, *Coch.*). The other division comprises the rest of the sac. The two correspond respectively to the cochlea and the vestibule of the bony labyrinth, including with the vestibule the semicircular canals; we may speak of them as the cochlear and vestibular portions of the sac. As we saw in studying the cranial nerves the auditory nerve (§ 618), though usually spoken of as one nerve, really consists of two nerves, different in origin, in ending, and to a certain extent in structure; one of these two, distributed to the cochlear division of the membranous labyrinth, we called the cochlear nerve, the other, distributed to the vestibular division, we called the vestibular nerve.

The vestibular division of the membranous labyrinth consists of an oval sac, about 6 mm. long, the *utricle* (utriculus) (Fig. 186, *U*), and lying below this a smaller, 3 mm. in diameter, more spherical, though somewhat oval flattened sac, the *saccule* (sacculus) (Fig. 186, *S*). Into the utricle open both ends of each of the

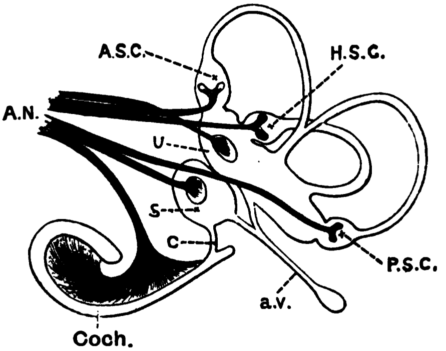

FIG. 186. THE MEMBRANOUS LABYRINTH AND THE ENDINGS OF THE AUDITORY NERVE.

**The figure is wholly diagrammatic, and is introduced as giving a simpler view of the essential parts of Fig. 185; it should be used only in conjunction with that.**

**U. utricle. S. saccule. A.S.C. Superior (or anterior), P.S.C. posterior, H.S.C. horizontal, semicircular canals.**

**Coch. The canalis cochlearis represented as a tube partially unrolled. c. canalis reuniens, joining the saccule with the canalis cochlearis. a.v. ductus endolymphaticus, shewing its origin from both saccule and utricle, and its dilated blind end, the saccus endolymphaticus.**

**A.N. The auditory nerve ending in the cristæ of the ampullæ, in the maculæ of the utricle and saccule, and along the whole length of the canalis cochlearis. The branch of the vestibular division of the nerve ending in the saccule remains in close contact with the cochlear division, longer than does the rest of the vestibular division ending in the utricle and ampullæ.**

three semicircular canals. These are disposed in the three planes of space. One (Fig. 186 *H.S.C.*) lies in a horizontal plane, and is called the *horizontal* or, since its hoop is directed outwards, the *external* semicircular canal. The other two lie in two vertical planes at right angles to the above. One lying in a vertical plane more or less parallel to the median plane of the head has its hoop directed backwards, and hence is called the *posterior* canal (*P.S.C.*); the other lying in a vertical plane more or less parallel to the transverse plane of the head has its hoop directed upwards, and hence is called the *superior* canal (*A.S.C.*). The three planes in which the three canals lie are placed with great exactitude at right angles to each other; they do not however coincide with the three planes of the head (sagittal or horizontal, median, and frontal or transverse) but make angles with these.

Each canal, at one of the ends by which it opens into the utricle, is dilated into a flask-shaped swelling, the ampulla, Figs. 185, 186), but at the other end does not shew any such marked swelling. The two ends of the two vertical canals, superior and posterior, which do not bear ampullæ, join together into a common canal (Fig. 185 *X.*) before they open into the utricle, but both ends of the horizontal canal are separate. Hence the canals, taken together, open into the utricle by five openings, three of which are marked by ampullæ, two are not.

The saccule, though lying close to the utricle, is wholly distinct from it and indeed is separated from it to a certain extent by a bony partition stretching inwards from the bony envelope; the cavity of the one has no direct communication with that of the other. An indirect communication is however supplied by the *ductus endolymphaticus* (Figs. 185 *d.e.* 186 *a.v.*) which formed by the union of a narrow tube, springing from the utricle with a wider one leading from the saccule, runs inwards towards the median line, in a canal hollowed out of the petrosal bone, and ends in a flattened sac, *saccus endolymphaticus* (Fig. 172 *s.e.*), placed in the cavity of the skull and supported between two layers of the dura mater. Through this hollow tube the cavity of the utricle is made continuous with that of the saccule.

From the saccule there starts also another narrow tube, the *canalis reuniens* (Fig. 186 *c.*), which opens into the canalis cochlearis, or cochlear division of the membranous labyrinth; by this the cavity of the vestibular division of the sac is made continuous with that of the cochlear division.

§ **822.** The wall of the membranous labyrinth consists throughout of an epithelium, modified in certain places into auditory epithelium (§ 808) and of a connective tissue or dermis, on which this epithelium rests. Around this dermis is developed the lymphatic cavity, lined with lymphatic epithelium (§ 809) and filled with perilymph, the outer wall of the cavity being furnished by connective tissue continuous with the periosteum of the bony envelope. The contour of the bony labyrinth follows in a general way only, not closely the contour of the membranous labyrinth; hence the perilymph space is not uniform but irregular. In some places, as for instance in the convexities of the semicircular canals, and where the nerves join it, the membranous labyrinth is fixed to the bony envelope, the periosteum of the latter being continuous with the dermis of the former or broken only by small lymph spaces. And where in other situations the perilymph cavity is large, it is much subdivided, in some places more than in others, by bridles and bands of connective tissue. Where the vestibule abuts on the median wall of the tympanum, in the situation of the fenestra ovalis, which is placed over against the line of division of utricle and saccule (Fig. 172) the space contains few such bridles, and here a considerable portion of the perilymph is gathered into what is sometimes spoken of as the 'cisterna.' In the hoops of the semicircular canals the membranous canal, much smaller in section than the bony canal, seems imbedded in the connective tissue of the latter, leaving a considerable space, broken by some few bridles, for the perilymph. In other places the bands of connective tissue, passing from the inner lining of the bony envelope to the walls of the membranous sac, are so abundant that the perilymph space becomes a labyrinth of small irregular passages. Nevertheless, however broken up, the whole perilymph space of the vestibular division of the ear is a continuous space, and the pulses given to it by the movements of the stapes sweep over the whole of it.

§ **823.** The auditory nerve, both the vestibular and the cochlear division, plunging into the floor of the cranium together with the facial nerve and the nervus intermedius by the canal known as the *meatus auditorius internus* (Fig. 173 *m.i.*), and traversing some compact bone continuous with the compact shell of the bony labyrinth, reaches the labyrinth at the open angle between the base of the cochlea and the vestibule. Here the cochlear nerve passes to the cochlea in a way which we shall presently describe. The vestibular nerve consists of two branches; one (ramus superior), lying above the other, is distributed to the utricle, and to the superior and horizontal semicircular canals, the other lying beneath the former ends in the saccule and in the posterior semicircular canal. In the utricle the nerve comes into connection, in a manner which we shall study in detail, with an area of modified auditory epithelium in the form of an oval low swelling, the *macula acustica* (Fig. 185 *m.u.*), and the connection of the nerve with the saccule is likewise in the form of a *macula* (Fig. 185 *m.s.*); the maculæ of the utricle and of the saccule are the only parts of these two structures in which the epithelium has any connections with the auditory nerve. In the case of each of the semicircular canals the nerve is in connection with a part, and a part only, of each ampulla. The area of modified auditory epithelium has in each ampulla the form of a forked or horse-shoe shaped ridge placed athwart the long axis of the ampulla and projecting into the interior; it is called a *crista acustica* (Figs. 185 *cr.p.*, *cr.s.*, *cr.h.*, 186). Hence the vestibular nerve ends exclusively in the macula acustica of the utricle, the macula acustica of the saccule, and the crista acustica of each of the three ampullæ. The superior branch before it ends in the utricle and superior and horizontal canals bears a ganglion of nerve cells. The median branch to the saccule likewise bears a ganglion which is more or less continuous with the ganglion of the superior branch, and the division which the same branch gives off to the posterior canal bears a group of nerve cells just before it joins its crista.

§ **824.** The cochlea may be considered as a prolongation of the vestibule in the form of an elongated cone; and indeed in some of the lower animals, in birds for instance, it is a short blunt cone. But it differs very widely from the rest of the labyrinth; and its special features may be broadly considered under three heads.

In the first place, the elongated, almost tubular, bony cone is not straight, but twisted closely on itself in two and a half whorls (Fig. 173), and the whorls grow together so as to form a short cone, the markings of the whorls being visible on the outside after the fashion of a gasteropod shell; hence the name. In the natural position in the head the cochlea is nearly horizontal, with the beginning of the first whorl at the base abutting on the median wall of the tympanum and with the apex directed forwards, and towards the median line; but when we are dealing with it by itself it will be convenient to consider it as if it were vertical in position with the apex above and the base below. The axis, or 'modiolus' as it has been called, round which the whorls are coiled differs from the walls of the whorls themselves in being formed of spongy, not compact bone, and is traversed by canals for the passage of the cochlear nerve, which entering it at the base from the meatus internus, ascends along it to the apex giving off fibres as we shall see all the way along.

In the second place, in the vestibule and semicircular canals the membranous labyrinth hangs, for the most part, loose within its bony shell, supported by irregular bridles, or is so attached that in any case there is no very definite arrangement of the perilymph space in relation to the sac which it surrounds; in the cochlea on the contrary a very definite arrangement obtains. This is best seen in a vertical section of the cochlea, in which the whorls are cut transversely in succession. The whole lumen of the coiled bony tube (Fig. 187) is seen to be roughly circular in section. Within this lies the canalis cochlearis (*C.Chl.*), the tubular continuation of the membranous labyrinth. This however is not, as in the semicircular canals, round or oval, but triangular in section. It is moreover so placed that while the base of the triangle is firmly attached to the outer wall of the bony tube, no perilymph space lying between the two, the apex of the triangle is also attached to the end of a thin sheet of bone (*Lam. sp.*) which projects outwards into the tube from the axis for some considerable distance. The triangular canalis cochlearis and the projecting sheet of bone thus completely divide the perilymph space of the tube into two spaces, one above and one below (the cochlea being supposed to be placed vertical).

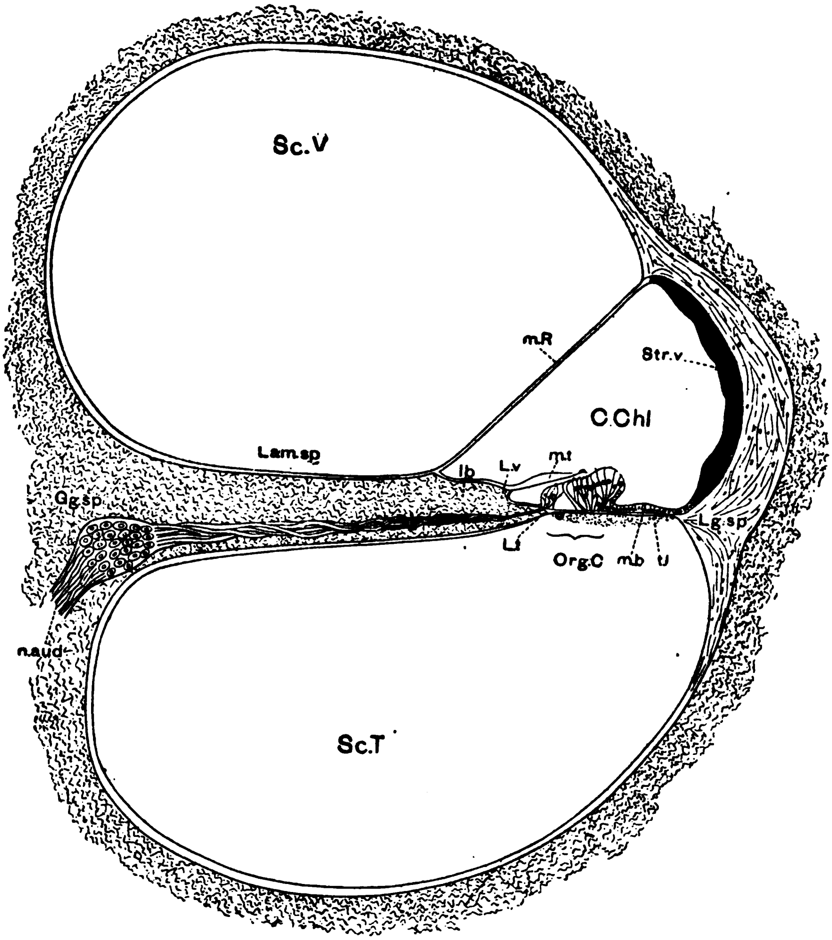

Fig. 187. Diagram of a transverse section of a Whorl of the Cochlea.

*Sc. V.* Scala vestibuli. *Sc.T.* Scala tympani. *C. Chl.* Canalis cochlearis.

*n.aud.* auditory nerve. *Gg.sp.* Spiral ganglion. *Lam.sp.* Lamina spiralis. *lb.* limbus. *L.v.* labium vestibulare. *Lt.* labium tympani. *m.R.* membrane of Reissner. *Lg.sp.* spiral ligament. *Str.v.* stria vascularis. *Org.C.* organ of Corti. *m.b.* basilar membrane. *t.l.* lymphatic epithelioid lining of the basilar membrane on the tympanic side. *m.t.* tectorial membrane.

These two spaces moreover are each entire, not being broken up or subdivided in any way by bridles or bands of connective tissue. Such an arrangement obtains all the way along the successive whorls except at the extreme top and extreme bottom. The projecting sheet of bone, as it is traced from the bottom to the top, describes a spiral, and hence is called the *lamina spiralis.* The canalis cochlearis also describes a spiral, winds in fact like a turret staircase, as do as well the two perilymph spaces, and the latter are hence called *scalæ.* The one lying above the canalis cochlea, when followed to the bottom of the cochlea is found to be continuous with, to open freely into, the perilymph space of the vestibule; hence it is called *scala vestibuli* (*Sc. V.*). The one lying below the canalis cochlearis ends blindly at the bottom of the cochlea, but in the bony wall of its blind end is an orifice, which we have already spoken of as the fenestra rotunda, the membrane covering which shuts off the scala in question from the cavity of the tympanum; hence this scala is called the *scala tympani* (*Sc. T.*). The canalis cochlearis thus lying between these two scalæ is sometimes called the *scala media;* but this name is undesirable since the canalis cochlearis being a part of the membranous labyrinth, a derivative of the otic vesicle, differs essentially in nature from the two scalæ, which are merely lymphatic, perilymph spaces.

The whole tube of the cochlea diminishes in size from the bottom of the lowermost whorl to the top of the highest; but the diminution affects the two scalæ alone, and the scala tympani more rapidly than the scala vestibuli; the canalis cochlearis so far from growing less, increases, except at the very top, from below upwards and especially, as we shall see, in the dimensions of one of its sides. At the top the lamina spiralis comes to an end, finishing off in the form of a hook, *hamulus,* and the canalis cochlearis suddenly diminishing ends blindly. Beyond the tip of the canalis cochlearis, the scala vestibuli which formed its roof, becomes, by a round orifice, *helicotrema,* continuous with the end of the scala tympani which formed its floor; here, and here alone does the one scala open into the other; and by this connection only has the fluid in the scala tympani access to the scala vestibuli and so to the perilymph space surrounding the vestibular portion of the labyrinth. The pulse which each thrust of the stapes at the fenestra ovalis imparts to the perilymph of the vestibule at the cisterna, passes into the scala vestibuli, and must either be transmitted to the scala tympani across the canalis cochlearis or must travel along the scala vestibuli to the apex of the cochlea, and down the whole length of the scala tympani before it breaks on the membrane of the fenestra rotunda.

If then the bony tube of the cochlea were unrolled and made straight it would appear as a tube diminishing to a pointed end; the lamina spiralis would appear as a longitudinal plate running along the whole length of the tube, and partially dividing it lengthways into two, while the canalis cochlearis would appear as a smaller tube, of triangular section, slid into the larger tube in such a way that the apex of the triangle all the way along touched the edge of the lamina spiralis, and the base all the way along was adherent to the opposite side of the main tube, thus separating completely the scali vestibuli on the one side from the scala tympani on the other. Only at the pointed end of the main tube would the canalis cochlearis be wanting, and here the two scalæ would run into each other.

The third great feature of the cochlea is that the auditory nerve is connected with the canalis cochlearis, not in a circumscribed patch, macula, or ridge, crista, but along its whole length; and there is accordingly an area of modified auditory epithelium along the whole length of the canal from close to the bottom of the undermost whorl to the tip, or nearly to the very tip of the topmost whorl.

The three sides of the canalis cochlearis differ markedly in structure and appearance. We shall study the details of these later on; meanwhile we may say that the wall which separates the canal from the scala vestibuli is a thin membrane (Fig. 187 *m. R.*), known as the *membrane of Reissner*, the epithelium on which lining the canal is of a simple character; that the epithelium which lines the base of the triangle, firmly attached to the bony wall, is also simple in character: but that a part of the epithelium lining the wall which separates the canalis cochlearis from the scala tympani is, along the whole length of the spiral, modified auditory epithelium and is known as the *organ of Corti* (Fig. 187, *Org. C.*).

The auditory, cochlear nerve, leaving the meatus internus, passes up the axis of the cochlea. As it ascends it gives off fibres passing outwards in a spiral manner into the lamina spiralis (cf. Fig. 185), which, thick towards the central axis, thins out towards its attachment to the canalis cochlearis. As these fibres traverse the lamina on their way outwards, numerous bipolar nerve-cells appear on their course, thus forming along the whole length of the spiral a continuous spiral ganglion, *the ganglion spirale* (Fig. 187, *Gg. sp.*). Having passed this ganglion and having reached the edge of the lamina spiralis, the fibres pass into and become connected, in a manner presently to be described, with the auditory epithelium of the organ of Corti.

We may now turn to the minute structure of the membranous labyrinth and its auditory epithelium, but before doing so it will be well to recall the position in relation to the tympanic cavity of the several parts of the internal ear which we have just described. The whole internal ear lies to the median side of and forms in part the median wall of the tympanic cavity. Nearly opposite the middle of the tympanic ring and membrane, the median wall of the tympanum is marked by an elevation (the promontorium), (cf. Fig. 176) which corresponds to the base of the cochlea, and which overhangs the depression leading to the fenestra rotunda. From this base the cochlea placed nearly horizontally, and thus nearly at right angles to the median wall of the tympanum, runs forwards inclining to the median side, the apex abutting on the bony wall of the Eustachian tube. Above the promontory the fenestra ovalis marks on the tympanic wall the position of the projecting portion of the vestibule; from this the semicircular canals project backwards and laterally, in their several planes, the ampulla of the superior and external canal forming a projection on the wall of the epitympanic cavity above the fenestra ovalis. The auditory nerve entering, in company with the facial nerve, on the median side in the open angle between the base of the cochlea and the vestibule, is distributed, as we have seen, to both these structures.

### *The Vestibular Labyrinth.*

§ **825**. Little need be said concerning the minute structure of those parts of the vestibular division of the labyrinth with which the auditory nerve makes no connections. The epithelium consists of a single layer of cells which are for the most part flat and polyhedral, though they differ somewhat in form and in other features in different regions. The epithelium rests on a thin connective tissue basis known as the "tunica propria;" this is hyaline, and except for some fibrillation or striation more obvious in some parts than in others, appears to be structureless; nuclei are absent from it and blood vessels do not pass into it. This tunic, which in the semicircular canals, in man, is with its epithelium frequently raised into irregular papillæ or warts, rests on an outer coat of vascular connective tissue, in some places continuous with, in others connected by bridles with the periosteum of the bony envelope. The spaces between the bundles of connective tissue of this coat gradually open out into the general perilymph cavity; it and they are lined with lymphatic epithelioid plates. The fluid (perilymph) contained in them, though it is not ordinary lymph, being viscid through the presence of mucin, finds access along the sheath of the auditory nerve into the subdural and subarachnoid spaces of the brain.

§ **826**. The three cristæ acusticæ are as we have said ridges projecting crosswise into the cavities of the ampullæ to which they respectively belong, each ridge being formed partly by a developement of the tunica propria and underlying connective tissue into a thick cushion of somewhat peculiar nature, and partly by an increase in the epithelium which, thick on the top of the ridge, gradually thins away at the sides.

Immediately below the epithelium the connective tissue cushion, especially at the top of the ridge, consists of a hyaline or faintly fibrillated ground-substance, traversed by blood vessels, but free from nuclei. Lower down scattered nuclei or rather connective tissue corpuscles make their appearance, but the ground-substance in which they lie remains for the most part hyaline, the tissue having an aspect not unlike that of cartilage. Still lower down the groundwork is broken up, in the ordinary way, into bundles of connective tissue. The branchlet of the auditory nerve, reaching the ridge at its base, not far from its middle, spreads out fanwise into nerve-fibres and bundles of nerve-fibres, which in a more or less plexiform manner run vertically upwards towards the summit of the ridge along its whole length. Hence in a transverse section of the ridge the nerve-fibres are seen ascending, in a vertical direction, through the connective tissue cushion to the epithelial cap, in which they are lost to view. So long as it remains in the connective tissue cushion each fibre retains all its constituents, neurilemma, medulla, and axis cylinder; upon entering the epithelium it loses as we shall see its neurilemma, and in most instances its medulla.

In a vertical section of a ridge, the thickened epithelium forming a cap to the ridge is seen to have special characters

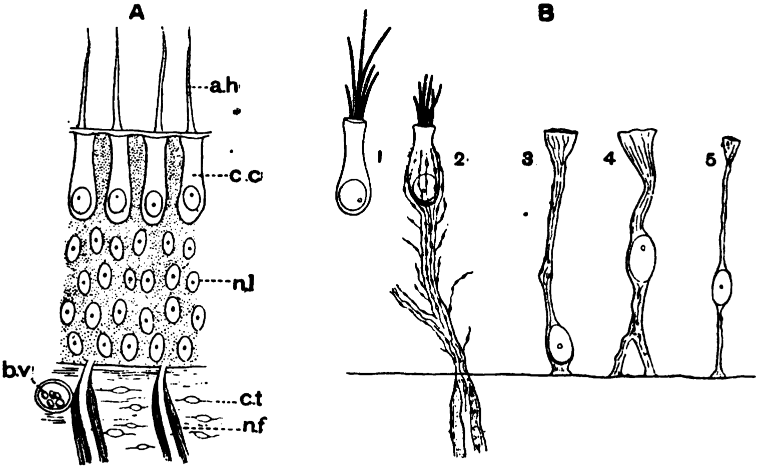

FIG. 188. DIAGRAM TO ILLUSTRATE THE STRUCTURE OF A CRISTA OR A MACULA.

A. a portion of a crista seen under a low power, shewing *c.c.* the cylinder cells, with *a.h.* auditory hairs, and *n.l.* the nuclear layer, the nuclei being diagrammatically shewn as if imbedded in a uniform ground-substance. *ct.* the connective tissue corpuscles of the dermis with *b.v.* a blood vessel, and *n.f.* nerve-fibre, the latter being shewn entering into the epithelium as a simple axis cylinder.

B. cylinder and rod cells. 1, an isolated cylinder cell. 2, the same surrounded with a nest of nerve-fibrillæ proceeding from a nerve-fibre. 3, 4, 5, various forms of rod-cells.

which are maintained from some little distance down the sides, and then almost suddenly cease. This is the *auditory epithelium*, and with this alone do the nerve-fibres make connections. Seen *in situ* (Fig. 188 A) this epithelium appears to consist of an outer row of cylindrical or columnar cells (*c.c.*), forming the free surface, and between this and the tunica propria, of a part calling to mind the nuclear layers of the retina, since it appears to be composed of nuclei (*n.l.*) closely packed together; we may speak of it as "the nuclear layer." From the free surface of this auditory epithelium a number of elongated, rigid, spoke-like processes (*a.h.*), of great length in some animals such as fishes, but shorter in man, project into the cavity of the ampulla; these are the *auditory hairs.* According to some authors at all events the free surface of the epithelium is guarded by a cuticular membrane, pierced for the passage of the auditory hairs.

At some little distance down the sides of the ridge, the nuclear layer disappears, as do also the auditory hairs; the auditory epithelium is almost suddenly transformed into a single layer of epithelial cells, which differ chiefly from the epithelial cells forming the general lining of the labyrinth, in that they are tall, cylindrical and large, with the cell substance rich in granules. These cylindrical cells, which in no way enter into connection with the fibres of the auditory nerve, gradually change at some distance from the auditory epithelium into the flat polyhedral cells of the general lining.

In hardened and prepared specimens* the auditory hairs appeared to be imbedded in a cap of mucous or fibrinous material. This, which has been called the "cupula," is supposed to be an artificial product, the result of a coagulation of the endolymph, and not to exist during life.

Contrary to what occurs in an epithelium elsewhere, the blood vessels instead of being absolutely confined to the connective tissue basis or dermis pass occasionally into the epithelium itself, and form loops among the cells; as we shall see this also occurs in the cochlea.

§ 827. The features which we have just described may be recognized without any great difficulty in sections of ampullæ prepared in various ways; but considerable difference of opinion obtains as to the exact nature of the constituent elements of the epithelium, and especially of their relations to the nerve-fibres; nor is the existence of a difference of opinion to be wondered at when the difficulties of investigation, greater perhaps than in any other histological subject, are borne in mind.

According to one view, the auditory epithelium consists of two kinds of cells. The one kind (Fig. 188 B, 1, 2) is a cell cylindrical in form or rather flask-shaped, with a flat top forming part of the free surface of the epithelium, and a conical but rounded base reaching less than half-way down the thickness of the epithelium.

The cell substance, very delicate in nature, contains a number of granules, and bears near the base a large, conspicuous, spheroidal nucleus. From the free surface there projects a bundle of long stiff hairs, the auditory hairs, which often stick together in the form of an attenuated cone. Cells of this kind may be called *hair-cells*, or for reasons which we shall see directly, *cylinder cells*.

The other kind of cell (Fig. 188 B 3, 4, 5) possesses a nucleus, smaller than that of the cylinder cell and having the form of a short ellipsoid, placed vertically; around this nucleus lies a relatively small quantity of cell substance, delicate like that of the cylinder cells but probably of a different nature. This scanty cell body is prolonged upwards between the cylinder cells as a rod-shaped process terminating abruptly at the surface, and stretches in the opposite direction as a process which, frequently but not always branched and irregular, reaches to and ends at the surface of the dermis. These *rod cells* or *spindle cells* are much more numerous than the cylinder cells, and their nuclei are placed at different levels, some close upon the dermis, others at different distances from it up to the level of the bases of the cylinder cells. The nuclei of these rod cells thus occupy the space between the bases of the cylinder cells and the dermis; they form in fact the nuclear layer spoken of above. It should be added that the nuclei which form a row immediately above the dermis are regarded by some authors as belonging to cells differing from the rod cells, their cell substance being said to be confined to the neighbourhood of the nucleus, and not to extend to the surface of the epithelium; these are spoken of as *basal cells*.

According to the view which we are relating, a nerve-fibre of the auditory nerve after traversing the auditory cushion (Fig. 188 A) passes into the epithelium and losing both neurilemma and medulla, though sometimes retaining the latter for a short distance, makes its way as a naked axis cylinder between the rod cells, taking sometimes a vertical, but often a more horizontal direction. In its course it gives off fine lateral irregular branches (Fig. 188 B 2), often divides, is frequently very distinctly fibrillated, and eventually ends in a nest or brush of fibrillæ, into which fits the conical base of a cylinder cell. The nerve-fibres appear to make no connections with the rod cells, which are hence regarded as of the nature of supporting or subsidiary structures; the cylinder cells alone, and according to this view it is these which bear the auditory hairs, are to be looked upon as the functional terminal organs of the fibres of the auditory nerve.

§ **828.** The maculæ acusticæ, both that of the utricle and that of the saccule, resemble the cristæ so far as essential features of structure are concerned. In them as in the cristæ both the dermis and the epithelium are thickened, but the elevation thus caused is in the form of a low swelling, not a steep ridge. The epithelium, which bears auditory hairs, consists of cylinder cells and rod cells, and the fibres of the auditory nerve enter into and are lost among the cells in the same way as in the cristæ. Perhaps the most conspicuous difference is that in the maculæ the auditory hairs are distinctly shorter than in the cristæ. Above each macula lies a fibrinous mass, not unlike the cupula, but having the form of a flat membrane; it is stated however to be a natural structure and not, like the cupula, an artificial product. There are no essential differences in structure between the macula of the utricle and that of the saccule. So far as we may permit ourselves to draw from structural features inferences concerning function, we may conclude that both the semicircular canals and the utricle with the saccule perform very much the same function; there is, so far as structure is concerned, nothing to indicate that the afferent impulses started in the cristæ differ from those started in the maculæ.

§ **829**. The endolymph, which we may look upon as secreted by the epithelium lining the membranous labyrinth and so far differing in origin from perilymph, resembles nevertheless that fluid very closely, containing however rather less solid matter. It is to a certain extent viscid, apparently owing to the presence of mucin.

In both the utricle and saccule are suspended in the endolymph crystalline bodies composed of calcium carbonate, with traces of other salts and with 25 p.c. or less of organic matter. In man and the higher animals, though varying in size, they are small crystals, generally rhombic or octohedral; and are then generally called *otoconia.* In some of the lower animals, for instance fishes, they form large masses, and are then generally called *otoliths.* The otoliths, and for the most part the otoconia, are confined to the utricle and saccule, and are usually found imbedded in the membrane spoken of above, which is hence sometimes called the "otolith" or "otoconial membrane." Otoconia may however occasionally be found in the ampullæ, or even in the perilymph chambers of the cochlea.

## *The Cochlea.*

§ **830**. As we have seen, the canalis cochlearis is a long spiral tube triangular in section, the apex of the triangle being attached to the edge of the spiral lamina, and the base to the opposite wall of the bony canal. In a dried specimen the bony spiral lamina ends in a thin edge, but in the fresh state the edge is thickened by connective tissue into a projection of peculiar form called the *limbus* (Fig. 187 *lb.*), which presents two edges, placed one above the other and seen in vertical section as two lips separated by a groove. The upper lip, which when looked at lengthways is seen to end in a number of projections or teeth, "auditory teeth," is called the *vestibular lip, labium vestibulare* (Fig. 187 *Lv.*, 189 *l.v.*), the lower lip is called the *tympanic lip, labium tympanicum* (187 *Lt.*, 189 *l.t.*), and the groove between them is called the *spiral groove, sulcus spiralis.* The vestibular lip and upper portion of the limbus is composed of a somewhat peculiar connective tissue, consisting of a homogeneous matrix in which are imbedded corpuscles; this is covered, except over the auditory teeth themselves, by a thin layer of flat epithelial cells, and deeper down passes into the bony tissue of the lamina. The vestibular lip serves for the attachment of the structure known as the *tectorial membrane, membrana tectoria* (Fig. 187, 189 *m.t.*). The tympanic lip, jutting farther outwards than does the upper lip, is the more direct continuation of the bony spiral lamina, and ends in an even edge composed of connective tissue which serves for the attachment of the *basilar membrane* (Figs. 187, 189 *m.b.*).

The membrane of Reissner, stretching across from the limbus of the spiral lamina to the opposite wall and so forming the vestibular wall of the canalis cochlearis (Fig. 187 *m.R.*), is a thin membrane, the basis of which is a sheet of homogeneous or obscurely fibrillated connective tissue, continuous on the inner, median side with the connective tissue of the limbus and on the opposite side with the periosteum of the bony shell of the cochlea. On the side looking towards the scala vestibuli this basis is covered with a single layer of lymphatic epithelioid plates; on the opposite side, in the cavity of the canalis cochlearis, it is covered with a single layer of flat polygonal cells, similar to those lining the non-auditory part of the vestibule, and like them presenting minor differences between themselves, some cells being more granular than others.

The periosteum which lines the whole of the bony canal of the cochlea, and which over the limbus may be supposed to be represented by the peculiar connective tissue spoken of above, is on the outer side, where the base of the triangle of the canalis cochlearis is attached, developed into a thick cushion (Fig. 187), consisting of interwoven bundles of connective tissue, among which are interspersed numerous branched cells imbedded in a clear matrix. Opposite the tympanic lip of the spiral lamina, the bundles of fibres of this tissue converge to form a projection, the *spiral ligament, ligamentum spirale* (Figs. 187, 189 *Lg. sp.*), which is attached to, or rather which passes into the outer edge of the basilar membrane.

This cushion of connective tissue extends above for a short distance into the region of the scala vestibuli, and for a greater distance below into the region of the scala tympani; it is however thickest and best developed opposite the canalis cochlearis. Here it is lined by the epithelium of that canal, but the characters of the epithelium in this region are somewhat special. The cells are cubical or even columnar, and frequently irregular in form; they are also granular and have the aspect of cells in which metabolism is active. The special characteristic however is that blood vessels which are abundant in the underlying connective tissue cushion traverse the line of demarcation between dermis and epithelium, and pass between the epithelial cells themselves, so that, in this region, a confusion between connective tissue and epithelial elements takes place. Owing to the peculiar prominence of the blood vessels this portion of the lining of the canalis cochlearis has been called the *vascular band, stria vascularis* (Fig. 187 *Str. v.*). We may probably regard it as secretory in function, analogous to the choroid plexus of the brain and the ciliary processes of the eye, and as taking at least a large part in furnishing the endolymph, which it must be remembered is useful not only for mechanical acoustic purposes, but also for the nourishment of the delicate auditory epithelium.

§ **831.** The remaining tympanic wall of the canalis cochlearis consists, like the membrane of Reissner, of a connective tissue basis with an epithelium derived from the epithelium of the otic vesicle on the one side, and with lymphatic epithelioid plates on the other; but part of the epithelium, namely a portion lying midway between the spiral lamina on the inside and the spiral ligament on the outside, is along the whole length of the spiral, except at the extreme ends, differentiated into auditory epithelium of remarkable characters; and the connective tissue basis possesses corresponding special features, as indeed does also the lymphatic epithelium.

At the extreme edge of the tympanic lip of the spiral lamina the ordinary bundles of fibres of connective tissue are gathered up into a thin sheet which stretches radially across to the spiral ligament, and there fuses again with the more ordinary connective tissue of that ligament. It is this sheet which is called the *basilar membrane* (Figs. 187, 189 *m.b.*). It may be regarded as consisting of two parts, one reaching radially from the tympanic lip to a point marked by the attachment of what we shall presently speak of as the feet of the outer rods of Corti, the other continued on from this point to the spiral ligament. In its first, more median part, the basilar membrane is a thin rigid sheet which, though distinctly fibrillated radially, cannot be said to be composed of definite fibres. In its second, more lateral part, the membrane becomes somewhat thicker, thinning however again as it approaches the spiral ligament, and is obviously composed of fibres, lying side by side and cemented by or imbedded in a homogeneous ground-substance differing in nature from the fibres themselves. The fibres, when isolated are stiff, bending at a sharp angle, not curling, and are easily broken.

On its tympanic side, the basilar membrane bears, resting on a thin layer of homogeneous ground-substance, a lymphatic epithelium (Figs. 187, 189 *t.l.*), the cells of which, often more than one layer deep, are spindle shaped, the cell substance being prolonged into filamentous processes taking a longitudinal, that is to say spiral, direction along the length of the canal. Near the tympanic lip, beneath what we shall speak of as the "tunnel" of the organ of Corti, a blood vessel, lying apparently in the midst of the epithelioid cells, may be traced for some distance up the spiral; this *vas spirale,* as it is called, serves to secure the due nourishment of the important structures lying over it.

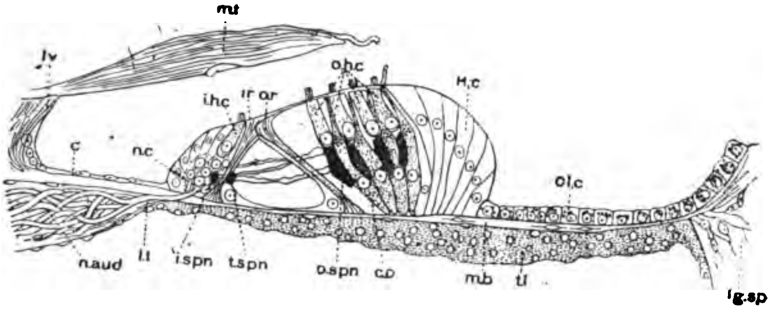

FIG. 189. DIAGRAM OF THE ORGAN OF CORTI. (After Retzius.)

*i.r.* inner rod of Corti, *o.r.* outer rod of Corti.

*i.h.c.* inner hair-cells, *n.c.* the group of nuclei beneath it. *o.h.c.* outer hair-cell, or cell of Corti, of the first row, *c.D.* its twin cell of Deiters; four rows of these twin cells are shewn.

*n.aud.* the auditory nerve perforating the tympanic lip *l.t,* and lost to view among the nuclei beneath the inner hair-cell. *i.sp.n.* the inner spiral strand of nerve-fibrillæ. *t.sp.n.* the spiral strand of the tunnel. *o.sp.n.* the outer spiral strand belonging to the first row of outer hair-cells; the three succeeding spiral strands belonging to the three other rows are also shewn. Nerve fibrillæ are shewn stretching radially across the tunnel.

*H.c.* Hensen's cells, *Cl.c.* Claudius cells, *m.b.* basilar membrane, *tl.* lymphatic epithelioid lining of the basilar membrane on the side towards the scala tympani. *lg.sp.* spiral ligament. *c'.* cells lining the spiral groove, overhung by *l.v.* the vestibular lip. *m.t.* the tectorial membrane; a fragment of it is seen torn from the rest and adherent to the organ of Corti just outside the outermost row of outer hair-cells.

§ **832.** On the side of the basilar membrane which looks towards the canalis cochlearis, the epithelium of the canal lies immediately on the membrane or is separated from it by a thin layer of homogeneous ground-substance in which here and there a corpuscle may be seen; and the part of this epithelium which is modified into auditory epithelium is called, as we have said, the *organ of Corti.*

At about the middle of the organ of Corti and forming as it were the keystone of its structure, are the bodies known as the *rods of Corti* (Figs. 189 *i.r., o.r.,* 190 B, B'), peculiarly modified epithelial cells, arranged along the length of the spiral in two rows, an inner row and an outer row. Each cell in each row has become, in large part, converted into a curved rod of peculiar shape, inclined at an angle to the basilar membrane in such a way that the inner rods and the outer rods lean against each other, their upper parts or "heads" being in contact, but their lower parts or "feet," which rest on the basilar membrane, being wide apart; hence they with a strip of the basilar membrane lying between their feet enclose a space, triangular in vertical section, forming along the length of the spiral the "tunnel" spoken of above (Fig. 189).

On the inner or median side of the row of inner rods, lies a single row of epithelial cells bearing hairs, the *inner hair-cells*, seen in vertical section as a single cell (Fig. 189 *i.h.c.*). At the base of the inner hair-cells lies a group of nuclei (*n.c.*) not unlike those forming the nuclear layer of a crista or macula; and just below these, the fibres of the auditory nerve pierce, as we shall see in detail presently, the tympanic lip in order to make connections with the epithelial organ of Corti. Next to the inner hair-cells, to the inner side, comes a row of tall columnar epithelium cells (seen in vertical section of course as a single cell); and this row is succeeded in the direction of the spiral groove, by other rows of cells diminishing in altitude until in the groove itself they thin away altogether, leaving bare of epithelium the auditory teeth which, as we have said, overhang the groove.

To the outside of the row of outer rods come four (or in certain parts of the spiral three or five) rows of complicated cells, which we may for the present speak of as *outer hair-cells* (Fig. 189 *o.h.c.*). These are succeeded outwards by a group of tall columnar or conical cells, of simple character, massed together in a group forming a hump to the outside of the outer hair-cells. These, which are called "Hensen's cells" (*H.c.*), are in turn succeeded outwards by shorter cubical or low columnar cells, called "Claudius cells" (*Cl. c.*), which at the spiral ligament pass into the epithelium of the stria vascularis. In both the cells of Hensen and those of Claudius, the cell substance is granular and is very often loaded with pigment or with material staining deeply with osmic acid or other reagents.

As we shall see, the row of inner and the rows of outer hair-cells are the only cells with which the fibres of the auditory nerve make any connections, and these with the rods of Corti are alone to be regarded as the functional terminal organs of the nerve; it is by means of these structures that the waves of sound are enabled to give rise to auditory impulses in the auditory nerve. The cells of Hensen and Claudius on the outside of the outer hair-cells, and the cells in the spiral groove on the inside of the inner hair-cells, have doubtless parts to play; but their function is probably in some way or other nutritive only, they are not immediately concerned in the production of auditory impulses.

§ **833**. The *inner rod of Corti* (Fig. 190 B) consists of a head, more or less round but with flattened sides, and of a thinner cylindrical body, or limb, which sloping with a gentle curve downwards and inwards ends in an enlarged foot cemented to rather than fused with the basilar membrane just at its beginning outside the tympanic lip of the spiral lamina. From the head a thin flat plate is continued outwards over the outer rods (Fig. 190 B *ph.*, D *i.r.h.*).

The *outer rod of Corti* (Fig. 190 B′) also consists of a head, the

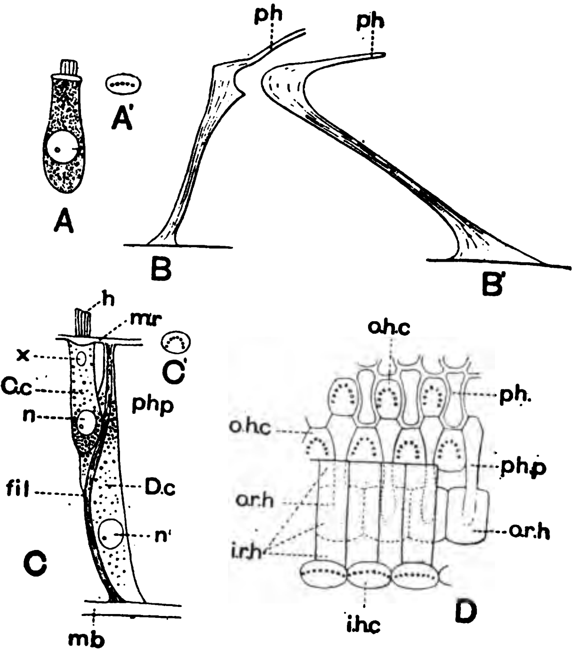

FIG. 190. DIAGRAM OF THE CONSTITUENTS OF THE ORGAN OF CORTI. (After Retzius.)

A. Inner hair-cells. A′, the head seen from above.

B. Inner, B′, outer rod of Corti, *ph.* (in each) phalangar process.

C. The twin outer hair-cell. *C.c.* cell of Corti, *h.* its auditory hairs, *n.* its nucleus, *x*, Hensen's body. *D.c.* cell of Deiters, *n′.* its nucleus, *ph.p.* its phalangar process, *fil.* the cuticular filament, *m.b.* basilar membrane, *m.r.* reticulate membrane.

C′. The head of the cell of Corti as seen from above.

D. The organ of Corti seen from above. *i.h.c.* the heads of the inner hair-cells. *ir.h.* the head and phalangar process of the inner rod. *o.r.h.* the head of the outer rod, with *ph.p.* its phalangar process, covered to the left hand by the inner rods, but uncovered to the right. *o.h.c.* the heads of the cells of Corti supported by the rings of the reticulate membrane. *ph.* one of the phalangæ of the reticulate membrane.

rounded surface of which directed inwards fits into a hollow supplied by the head of the inner rod, while the upper surface is prolonged outwards in the direction of the outer hair-cells as a long plate, the "phalangar process" (B′ *ph.*). To the head succeeds a slender cylindrical gently curved body or limb, which sloping downwards and outwards ends in an expanded foot cemented to the basilar membrane at some distance to the outer side of the attachment of the foot of the inner rod.

The substance of which the rods are composed is peculiar. In a perfectly fresh state the rods seem homogeneous or, especially in the region of the limb, obscurely striated; they are somewhat easily decomposed and are readily acted upon by reagents; under the influence of hardening reagents they become rigid, and the limb is then distinctly striated longitudinally. At each angle, formed by the limb and foot of the inner rod and of the outer rod with the basilar membrane, is seen a nucleus surrounded by ordinary protoplasmic cell substance, and a thin layer of the same cell substance is continued as a delicate lining up the limbs. The rods may be considered as portions of the substance of two cells, represented by the two nuclei just spoken of, which have become specially differentiated in nature, and in being differentiated have assumed a special form. They have been spoken of as 'cuticular' formations, and indeed the phalangar process of the outer rod is the beginning of a structure which may be considered cuticular and which, consisting of rings joined together by flat bars, or "phalangæ," stretches outwards so as to form a covering over the whole region of the outer hair-cells (Fig. 190 D). Through the holes of the rings of this *reticulate membrane, membrana reticulata* as it is called, the heads of the outer hair-cells project, and processes from cells which we shall presently describe as connected with or forming part of the outer hair-cells are attached to the bars between the rings. The word "phalangæ" means the poles on which a burden is slung between two men's shoulders; and the cells of the organ of Corti may be regarded as slung from the trellis work of the reticulate membrane, or perhaps more exactly slung between it and the basilar membrane. The whole reticulate membrane thus seeming to serve as a support to the outer hair-cells, may justly be regarded as cuticular; and if so we may regard the rods of Corti as cuticular also. It must however be remembered that the rods are very peculiar in nature; one might be inclined to compare them on the one hand with the hyaline border of a ciliated cell, and on the other hand with the outer limbs of the rods and cones of the retina.

The rods thus form along the length of the spiral of the cochlea a double row, inner and outer. In each row the heads are in contact, the adjoining sides being as we said flat; the phalangar processes of the outer row are also in contact with each other, side by side; and the outer heads fit into the inner heads. Hence when the organ of Corti is viewed from above (Fig. 190 D) along a portion of its length, this part of the organ very strikingly resembles the keys of a piano. The inner rods however are more numerous than the outer rods, in the proportion of 5·6 to 3·8, so that each outer rod is not exactly opposite an inner rod, but fits into more than one inner rod.

While, in the case of both inner and outer rods the heads are in contact sideways, that is to say along the length of the spiral, and the same is true of the expanded feet also, the more slender limbs are not in contact but leave spaces or clefts between every two rods in each row. Through these clefts nerve filaments, as we shall see, make their way from the region of the inner hair-cells into the spiral tunnel formed by the rows of inner and outer rods on each side and by the basilar membrane at the base, and beyond this, from the tunnel into the region of the outer hair-cells.

§ **834.** The *inner hair-cells* form a single row to the inner side of the inner rods. Each hair-cell (Fig. 190 A) bears much resemblance to, and may be regarded as analogous to a cylinder cell of a crista or macula. It is flask-shaped, ending below in a blunt cone, and bears in its lower part a large spherical nucleus. Its upper end, circular or oval in outline, has a hyaline border like that of a ciliated cell, and from this project a number, a dozen or more, not of long hairs but of short (5 $\mu$) rods, definitely arranged in a gentle curve (Fig. 190 A′), lying at about the middle of the free surface of the cell with the hollow of the curve looking inwards towards the spiral lamina. The substance of the cell is granular, but very watery and very delicate, readily shrinking and becoming deformed under the influence of reagents.

The pointed base of the inner hair-cell dips down into a group of nuclei, which form, as we have said, something like the nuclear layer of the crista or macula. There has been much difference of opinion about these nuclei, but they appear to belong to cells very like the rod cells of the crista and macula. The scanty cell substance round the nucleus is prolonged downwards as a thin process to or towards the tympanic lip and beginning of the basilar membrane and upwards also as a thin process, which running by the side of the inner hair-cells, ends apparently in a cuticular expansion. The nuclei may therefore be considered as belonging to supporting or subsidiary structures. The row of inner hair-cells abuts, on the inner side, on the heads of the inner rods, which thus afford a support to them on this side. On the other side, towards the spiral lamina, the hair-cells are supported by the elongated epithelial cells mentioned above as continuous with those lining the spiral groove and also by the supporting cells of the nuclear layer, the processes of the latter apparently passing also in between the hair-cells in the row, for the hair-cells though near together in the row do not absolutely touch.

§ **835.** The *outer hair-cells* are arranged as we have said in a series of rows between the outer rods of Corti and Hensen's cells, the number of rows along the greater part of the spiral being, in man, four. Each row is almost exactly like the others, and the description of any one row will apply to all the others. We have hitherto spoken of the cells as simply outer hair-cells, but each row is composed not of single cells in a file, but of twin cells or of pairs of cells. In each pair we may recognize a cell which bears hairs (or rather rods), the hair-cell proper, or *cell of Corti* (Fig. 190 C. *C.c.*) and a cell which does not bear hairs (or rods) the *cell of Deiters* (*D.c.*), the two cells in each pair being in close apposition or according to some observers actually united.

The cell of Corti very closely resembles an inner hair-cell. The body is flask-shaped, and ends in a blunt cone at some distance below the reticulate membrane, between it and the basilar membrane; near its end is placed a large spherical nucleus. The cell-body appears granular, especially at its lower part, but the granules seem to be superficial in position, and the greater part of the interior of the body appears to be of a fluid nature: hence the cell readily shrinks and becomes deformed under the influence of reagents. The upper end, circular in form, projects through, and is as it were grasped by a ring of the reticulate membrane (Fig. 190 D), and the free surface bears, like the inner hair-cell, a row of short rods, but these are arranged as a distinct horse-shoe or a semicircle, with the hollow of the curve looking inwards. The top portion of the cell supplies a hyaline border, and immediately below this is placed a peculiar nuclear looking body, called "Hensen's body" (Fig. 190 C *x.*).

The cell of Deiters (Fig. 190 C. *Dc.*) consists of a cell-body, the median portion of which is placed at the level of the lower end of the cell of Corti, so that this seems to rest on or according to some to be fused with it. From this body there stretches upwards a tapering process (Fig. 190 C. *php*), which joins the overlying reticulate membrane, and becomes attached to the phalangar bar lying to the outside of the ring encircling the head of its twin cell of Corti; it may be called the 'phalangar process.' Downwards the body is prolonged, slanting outwards, as a cylindrical process reaching as far as and becoming attached to the basilar membrane. This part of the cell bears a rounded nucleus (*n'*), and is, in the greater part of its extent, of a delicate nature and easily destroyed; but on its inside, looking towards the rod of Corti, the cell-substance is differentiated into a cuticular band or thread (*fil*), which below is cemented to the basilar membrane, and above may be traced into the upward phalangar process and so to the reticulate membrane. There seems good reason for regarding this cell of Deiters as a structure analogous to the rod cells of the crista and macula, but a structure more specially modified than are they. We may probably consider it, like them, to be essentially supporting or at least subsidiary in function, that is to say, not in itself giving rise to auditory nervous impulses but in some subsidiary way assisting the hair-cell proper, that is the cell of Corti, to do so. It will be observed that the cell of Deiters serves as a brace or tie between the reticulate membrane above and the basilar membrane below, while at the same time it is in such complete apposition to if not in continuity with the cell of Corti, that we may justly suppose molecular processes started in it to be readily communicated to that.

The first row of outer hair-cells is placed at some little distance from the outer rod of Corti, being separated from it by a space corresponding to the length of the phalangar process of the rod-head; but the succeeding rows follow close on each other, and the series is closed on the outside towards the spiral ligament by the group of Hensen's cells. The phalangar process of the inner rod is inclined somewhat upwards, and the same inclination is maintained by the reticulate membrane and the whole row of outer hair-cells, there being a gradual ascent from the inner hair-cells to the cells of Hensen.

§ **836**. *The cochlear nerve* reaches the organ of Corti through the spiral lamina. The centre of the base of the cochlea round which the first whorl winds is scooped out into a hollow, and from this a central canal, gradually narrowing, runs up the axis of the whorls. The cochlear nerve lies in the hollow and is continued up into the central canal; in its course it gives off from the hollow and from the central canal a series of bundles of nerve-fibres which pass radially into the spiral lamina, being like it arranged in a spiral. At the bottom the nerve is thick; it diminishes in bulk as each bundle is given off, and ends by giving off its last bundle near the top of the spiral.

On their way through the spiral lamina in a radiate direction all the bundles become connected with a collection of nerve cells, arranged in a spiral band, the *ganglion spirale*, lying in the spiral lamina (Fig. 187 *Gg. sp.*). The cells of this ganglion closely resemble those of a ganglion on the posterior root of a spinal nerve (§ 97); the nerve-fibres are however not connected with the cells by T pieces, since the cells are typically bipolar, the fibre entering the cell at one pole and issuing at the opposite pole. The issuing fibre as well as the entering fibre is medullated.

The fibres, issuing from the ganglion in bundles, break up into a loose plexus, and ascend obliquely towards the tympanum lip. As they approach the membranous, connective tissue end of the lip, the fibres are gathered into a series of more close set plexuses, which pierce the lip through a series of slit-like orifices, *foramina nervina*, and thus, as a series of bundles, enter the overlying epithelium in the region of the inner hair-cells. As they issue from the connective tissue of the lip the fibres lose neurilemma and medulla, and enter the epithelium as naked axis cylinders.

Concerning the farther course and ultimate endings of the nerve there is much diversity and uncertainty of opinion; but the following account is probably the one deserving the greater amount of confidence.

The axis cylinders, passing into the epithelium in the region of the nuclear layer beneath the inner hair-cells, split up into fibrillæ and bundles of fibrillæ. Some of these changing their course from a radiate to a longitudinal, spiral one, contribute to form a strand of fibrillæ which runs in a spiral along the length of the cochlea, in the nuclear layer at the base of the inner hair-cells, and may be seen in vertical sections as a group of dots in this position (Fig. 189 *i.sp.n.*); it is known as the *inner spiral strand.* Fibrillæ from this strand, or coming directly from the entering axis cylinders, invest the bases of the inner hair-cells with nests of fibrillæ, very similar to those which invest the hair-cells of the crista and macula.

Other fibrillæ passing between the limbs of the inner rods of Corti, give rise to a second spiral strand lying within the tunnel close to the inner rods (Fig. 189 *t.sp.n.*). This is known as the *spiral strand of the tunnel.*

Other fibrillæ again, possibly connected with or joined by fibrillæ from the tunnel strand just mentioned, traverse the tunnel in a radiate direction, pass between the limbs of the outer rods, and form beneath the bases of the outer hair-cells proper, that is the cells of Corti, at the level where the bodies of the cells of Corti and of Deiters join each other, four *outer spiral strands* (Fig. 189 *O.sp.n.*), one for each row of hair-cells. From these spiral strands or in connection with these spiral strands, fibrillæ invest the bases of the cells of Corti with nervous nests similar to those belonging to the inner hair-cells.

So far therefore as can be at present ascertained the fibres of the auditory nerve end in fibrillæ which form nests around both the inner and outer hair-cells; and if we accept the view laid down in § 827 we may say that the mode of ending of the cochlear nerve is fundamentally the same as that of the vestibular nerve. Whether the fibrillæ are actually continuous with the substance of the hair-cells, or whether the material of the one is only in close juxtaposition with the material of the other must be left for the present uncertain. We may however conclude that it is in the hair-cells, inner and outer, that auditory impulses are originated, and that the other parts of the organ of Corti are subsidiary in function, helping or guiding in some way the development of the nervous impulses, but not actually giving rise to them.

The space of the tunnel between the rods of Corti appears to be occupied by fluid, which gives support to the bundles of fibrillæ stretching across the tunnel. This space is continuous, through the clefts between the limbs of the outer rods, with the space between the outer rods and the first row of hair-cells, and so with the narrow spaces between the several rows of hair-cells. But the whole of this space is completely shut off from the endolymph space of the canalis cochlearis by the reticulate membrane above, by the closely packed epithelial cells on the inner side of the inner hair-cells to the inside, and to the outside by the closely packed cells of Hensen lying on the outside of the outermost row of outer hair-cells; it is also completely shut off from the scala tympani by the basilar membrane.

§ **837**. The organ of Corti is overhung by a peculiar structure projecting from the vestibular lip of the spiral lamina, and known as the *tectorial membrane, membrana tectoria* (Fig. 189 *m.t.*). It is in a fresh state soft and elastic, is fibrillated in radial direction, and indeed appears to be largely composed of fine fibres or fibrils; these resist the action of acetic acid. It begins on the surface of the limbus of the spiral lamina not far from the attachment of Reissner's membrane; it is thin over the vestibular lip, but beyond the free edge of the lip, overhanging the inner hair-cells and rods of Corti, it becomes thick, ending gradually in a thin and often ragged edge at about the zone of the outermost row of outer hair-cells. It is frequently pitted or otherwise sculptured on its under surface.

§ **838**. The features and the structure of the canalis cochlearis and especially of the organ of Corti differ in details in different mammals; the description given above applies to man. We said above that the number of rows of outer hair-cells was in man four; but in the lowermost turn of the spiral three only are present, and even in the upper turns, the number four is not constant; in places five rows are sometimes seen. In the majority of mammals there are three rows of outer hair-cells, but a fourth row is sometimes present.

In the same cochlea, the features differ along the length of the spiral, so that a vertical section from an upper whorl presents many differences when compared with a section from a lower whorl. We must not dwell on these differences: but we may call attention to what seems an important fact, namely that the basilar membrane, especially that outer part of it which reaches from the foot of the outer rods to the spiral ligament, increases in length from below upwards, except at the very top.

At the top of the spiral the organ of Corti becoming rapidly less conspicuous comes suddenly to an end; the inner and outer hair-cells and rods of Corti suddenly stop, and with them the fibres of the cochlear nerve stop also; the blind end of the canalis cochlearis is lined merely with epithelial cells of a simple character, the continuation of the cells of the spiral groove, of the cells of Claudius, and of the other cells lining the canal; the vascular band is continued a little way beyond the organ of Corti and then comes to an end too, and by thus ending indicates its functional connection with that organ.

At the other, lower extremity or beginning of the spiral, the organ of Corti similarly ceases, and the blind end or "cup" beyond the canalis reuniens, is, like the extreme top, lined by a simple epithelium.

Vertebrates below mammals do not possess an organ of Corti strictly so called; in the rudimentary cochlea of birds and reptiles a basilar membrane and hair-cells are present; but the rods of Corti are absent. As we pass in review the features of the membranous labyrinth in various vertebrates from the lowest upwards, we find the several parts becoming more and more distinct from each other; the saccule becomes more and more separate from the utricle and the semicircular canals, and the cochlea, which is at first a process of the saccule, becomes more and more distinct from it.

§ **839**. It may be worth while to call attention to the following data concerning the cochlea of man which have been obtained by careful partial measurements and calculations.

| | |
|---|---|
| Length of the Canalis cochlearis | 35 mm. |
| Length of the organ of Corti | 33·5 mm. |
| Radial width of the basilar membrane (measured from the entrance of the nerve-fibres to the spiral ligament) | |
| In the Basal whorl of spiral | ·21 mm. |
| „ Middle „ „ | ·34 mm. |
| „ Topmost „ „ | ·36 mm. |
| Number of perforations for nerve-fibres | 4000. |
| „ „ Inner hair-cells | 3500. |
| „ „ Inner rods of Corti | 5600. |
| „ „ Outer „ „ „ | 3850. |
| „ „ Outer hair-cells (in 4 rows) | 12000. |
| „ „ Fibres of the basilar membrane | 24000. |

## SEC. 3. ON AUDITORY SENSATIONS.

§ **840**. The vibrations which we call sound are transmitted as we have seen to the perilymph through the fenestra ovalis, by means of the tympanic membrane and chain of ossicles. The vibrations of the perilymph in some way or other, by help of the auditory epithelium, give rise in the fibres of the auditory nerve to auditory impulses, and these reaching the brain are developed into auditory sensations. Before we attempt to consider how the vibrations of the perilymph thus give rise to auditory impulses it will be convenient to adopt the plan which we pursued in the case of vision, and to deal first with some of the leading characters of auditory sensations such as can be ascertained by psychological methods.

We readily recognize two classes of sensations; the objective causes of the one class we speak of as *noises*, those of the other class as *musical sounds*. When we inquire into the physical features of the two classes we find that the vibrations which constitute a musical sound are repeated at regular intervals, and thus possess a marked periodicity or rhythm. When no marked periodicity is present in the vibrations, when the repetition of the several vibrations is irregular, the sensation produced is that of a noise. There is however no abrupt line between the two. Between a pure and simple musical sound produced by a series of vibrations each of which has exactly the same period, and a harsh noise in which no consecutive vibrations are alike, there are numerous intermediate stages. Much irregularity may present itself in a series of sounds called music, and in some of the roughest noises the regular repetition of one or more vibrations may be easily recognized. Still it will be desirable to consider the two classes as distinct, and it will be convenient to deal first with musical sounds.

§ **841**. The sensations which are produced by musical sounds possess three marked characters. In the first place, our auditory sensations like our other sensations, may be more or less intense; and the character in a musical sound which corresponds to the intensity of the sensation we call *loudness*. This is determined by the amplitude of the vibrations, by the amount of energy which is expended in producing the vibratory movements; the greater the disturbance of the air (or other medium) the louder the sound. Using the term 'wave' to denote the characters of the vibrations, the loudness of a sound is indicated by the *height* of the wave.

In the second place, we recognize a character which we call *pitch.* This is determined by the frequency of repetition of the vibrations, by the time taken up by each vibration; the greater the number of consecutive vibrations which fall upon the ear in a second, the shorter the time of each vibration, the higher the pitch. Hence the pitch of a sound is indicated by the *length* of the wave, a low note having a long, a high note a short wave-length. We are able to distinguish a whole series of musical sounds of different pitch, from the lowest to the highest audible note.

In the third place, we distinguish musical sounds by what is usually called their *quality* (*timbre*); the same note sounded on a piano and on a violin produces very different sensations, even though the two instruments give rise to vibrations having the same period of repetition. This arises from the fact that the musical sounds generated by most musical instruments are not simple but compound vibrations; the instrument sets going in the surrounding air not one series only of vibrations of one wave-length, but several series of different wave-lengths; as we shall see, however, the several vibrations travel through the air, not as a group of waves but as one compound wave. When the note C in the bass clef is struck on the piano, and we analyse the total sound, we find that it can be resolved partly into a series of vibrations with a period characteristic of the pure tone of C of the bass clef, and partly into other series of vibrations with periods characteristic of the C in the octave above (middle C), of the G above that, of the C of the next octave, and of the E above that. And the sensation which we associate with the sound of the C in the bass clef on the piano is determined by the characters of the complex vibration arising out of these several constituent simple vibrations. Almost all musical sounds are thus composed of what is called a *fundamental tone* accompanied by a number of *partial tones.* When a violin string gives out a musical note, the fundamental tone is produced by the string vibrating along its whole length, the partial tones by the string vibrating at the same time in segments or definite parts of the whole length; and so with other instruments; hence the name 'partial.' Since these partial tones have a higher pitch than the fundamental tone they are frequently spoken of as 'partial upper-tones or overtones' or simply as 'overtones.' The partial tones vary in number and relative prominence in different instruments and thus give rise to a difference in the sensation caused by the whole sound. Hence while a 'tone' is a single series of simple vibrations, a 'note' may be and generally is a number of series of different vibrations occurring together. While the fundamental tone determines the pitch of a note, the quality of the note is determined by the number and relative prominence of the partial tones.

If we compare auditory with visual sensations it is obvious that loudness of sound corresponds to brightness or luminosity of light; in both cases the terms denote the intensity of the sensation. We may perhaps compare the character of pitch, dependent on the wave-length of the sound vibration, to the character of colour dependent on the wave-length of the ray of light; and we may, in a general way, liken the auditory effect produced by a sound of a particular quality to the visual effect produced by an object which excites mixed colour sensations, owing to rays of several different wave-lengths falling at the same time on the retina; on examination, however, it will be found that the differences in these respects between the two sets of sensations are more striking than the resemblances.

§ **842.** In much the same way that rays of light of more than or of less than a certain wave-length are incapable of exciting the retina, our vision being limited to the range of the visible spectrum, waves of sound of more than or of less than a certain wave-length are unable to affect the ear so as to produce a sensation of sound. Vibrations having a recurrence below about 30 a second are unable to produce a sensation of sound; the note of the 16-feet organ pipe, 33 vibrations a second, gives us the sensation of a droning sound; a tone of 40 vibrations is quite distinct. Some authors, however, place the limit at 24 or even 15 a second. If waves of long wave-length are powerful enough we may feel them by the sense of touch, though not by that of hearing. What we have just said applies to vibrations which are simple, such as give rise to a pure tone; if the fundamental tone is accompanied by partial tones we may hear one or other of these, and are thus apt to say we hear the former when in reality we only hear the latter. As regards the limit of high notes, individuals differ very much from one another, but the limit for most persons is about 16,000. Some persons hear low sounds more easily than high ones, and *vice versâ.* This may be so pronounced as to justify the subjects being spoken of as deaf to low or high tones respectively, a condition which may be compared in a general way to colour blindness. In some cases of disease it has been found that there is inability to hear isolated groups of tones in the middle of the scale; in other cases there may be complete deafness except to one or more such isolated groups. The range in different animals differs very widely, the high notes of the instrument known as Galton's whistle, though inaudible to man, are distinctly heard by some other animals, for instance cats.

The limitations which are thus imposed on our hearing do not wholly correspond to the limitations of our vision. In the latter case the limits are fixed wholly by the capacities of the retina and cerebral centres; radiant rays of longer wave-length than the extreme visible red are able to get access to the retina through the dioptric apparatus though they are unable to excite visual impulses, or at least such visual impulses as can affect consciousness. In the case of hearing, though the auditory epithelium is probably, like the retinal structures, limited in its powers, narrower limits are fixed by the subsidiary acoustic apparatus; the tympanic membrane, extensive as is its range compared with that of most artificial membranes, cannot respond to all vibrations; and hence its powers fix the limits of hearing. The reason why we appreciate high notes more readily than low ones is probably to be referred to the tympanum rather than to the auditory epithelium. And the condition of the tympanal apparatus as affected by disease will determine the relative appreciation of low or high tones; in certain states of the tympanum the ear becomes unusually sensitive to high notes; an instance of this is seen in the paralysis of the stapedius muscle due to injury or disease of the seventh nerve.

§ **843.** We dwelt, in speaking of vision, on our power of appreciating differences of brightness or luminosity; we have a similar power of appreciating differences in loudness; and that relation between differences in the intensity of the stimulus and differences in the intensity of the sensation, which we spoke of as Weber's law (§ 747), holds good for hearing as well as for vision.

The power of distinguishing difference of pitch, the power of recognizing the difference between two notes of different pitch, and the appreciation of the qualities of various musical sounds which is built up on this, may in a general way be compared to acuteness of colour vision. It is however, as we have said, very different from that in many respects, and varies much more widely than does that. As is well known the difference in this power between different individuals, according as they have or have not a 'musical ear,' is very great. Some persons even though fairly sensitive to differences of loudness, are unable to distinguish two notes differing considerably in wave-length. On the other hand a well-trained ear can distinguish the difference of a single or even of a half vibration a second, and that through a long range of notes. As might be expected the power of appreciating difference of pitch is not the same for all audible notes. The range of an ordinary appreciation of tones lies between 40 and 4000 vibrations a second, *i.e.* between the lowest bass C ($C_1$ 33 vibrations) and the highest treble C ($C^5$ 4224 vibrations) of the piano; tones above and below these, even though audible, are distinguished from each other with great difficulty. The power of recognizing, and being able to name, a note when heard, is an extension of and based upon this power of recognizing differences of pitch, though not by itself exactly the same thing.

§ **844.** We said, in speaking of vision (§ 748), that, probably, several undulations falling in succession upon the retina were necessary for the development of a visual sensation. In like manner, in order that a distinct sensation of a musical sound may be developed, several, or at least more than one wave of sound must fall on the ear. The various observers are not agreed as to the lower limit of the number of vibrations necessary in order that the affection of consciousness may take the form of a definite musical sound; some place it at five, others higher, while it has been asserted that two vibrations are sufficient. When the vibrations are thus limited in number the sound, even though it is recognized as a musical sound, is not clearly appreciated; its pitch is not distinctly recognized. In such a case the recognition may be made more full and certain by increasing the number of vibrations; in order that we may appreciate the pitch of a sound the ear must receive a larger number of vibrations than are necessary merely to enable us to recognize that the sound is a definite one. Conversely even when the vibrations are too few to give rise to a sensation of a definite tone, consciousness is not wholly unaffected, an auditory sensation is produced, though it cannot be called one of tone. These facts indicate the complex nature of the nervous processes which form the basis of auditory sensations; we might say this of sensations in general, for similar results are observed in the case of all sensations.

§ **845**. As we said above (§ 840) noises are not sharply defined from musical sounds, they differ only in being more complex and less regular; and what has just been said in respect to musical sounds, holds good to a large extent for noises. We readily distinguish, in noises, difference of loudness; we may also in many cases recognize a dominance of pitch, due to the fact that among the multifarious vibrations certain groups of vibrations are repeated periodically; we distinguish a rumbling noise in which vibrations of slow recurrence are prominent from a harsh shrill noise in which rapid vibrations are similarly prominent; we also recognize qualities in noises, we distinguish one noise from the other by the characters of the predominant constituent vibrations. Owing to the fact to which we just now referred that in a musical sound the effect on consciousness is a summation of the individual effects of the several vibrations we are more sensitive to a musical sound of not too short duration, than to a noise involving an equal expenditure of energy. On the other hand the limit of the number of movements necessary to give rise to a sensation of noise is less than that required for a musical sound; a few vibrations insufficient in number to give rise to the sensation of a tone are able to give rise to an auditory sensation which we may call a noise, and probably one movement of the tympanic membrane might if ample enough give rise to such an auditory sensation. Moreover owing to the very irregularity of a noise, to the varied character of the constituent molecular movements, we have a very great range in distinguishing various noises; persons who have great difficulty in detecting different notes can often readily recognize differences in noises.

§ **846.** In treating of vision we dwelt at some length on the phenomena of exhaustion which make their appearance when the stimulus is continued. These occur in hearing also, and indeed are indicated by such common phrases as "a deafening noise;" but they are not so prominent as in vision, and do not so distinctly serve as the basis for theoretical discussions. They are best studied by means of musical sounds, since with these owing to their very nature the stimulation is more uniform than with noises. With almost any note, the sensation diminishes and finally disappears if the sound be maintained long enough; but the exhaustion comes on more rapidly with high than with low notes, especially with very high ones. If a sounding tuning-fork be held up to one ear, and then, just as the sound becomes inaudible be transferred to the other ear, the sound may be distinctly heard; the fresh untired sensory apparatus of the one side is sensitive to the vibrations which the tired apparatus of the other side can no longer feel. Or, if the tuning-fork which the tired ear can no longer hear, be replaced by one vibrating at the moment as far as can be arranged with the same intensity as it, but of distinctly different pitch, this will be heard; the first tuning-fork only tired certain parts of the sensory apparatus, those affected by vibrations of a certain period characteristic of the pitch of that tuning-fork, but left untired the parts of the sensory apparatus responding to the vibration of other periods, such as those of the second tuning-fork.

Again, the quality of a note struck on a musical instrument depends as we have seen on the presence of partial tones, having certain relations to the fundamental tone. Now, if immediately before striking a note on an instrument, choosing especially an instrument whose notes are 'rich' by virtue of the number or prominence of the partial tones, we cause one of the partial tones of the note to be sounded powerfully in the ear, the note when subsequently struck does not possess its full quality; it appears 'thin' or 'poor.' This is because the previous sounding of the partial tone has tired the particular part of the auditory apparatus with which we hear the partial tone, and in the whole sensation of the subsequent full note the constituent sensation corresponding to that particular partial tone is absent or at least is below its normal intensity. Thus we have in auditory sensations something analogous to the "negative image" of visual sensations.

We do not in hearing experience a sensation analogous to the visual sensation of white light, a simultaneous stimulation of the apparatus by vibrations of all kinds, and cannot therefore experience an auditory sensation corresponding to the visual sensation of black; the nearest approach perhaps to such a psychological condition is that in which we are placed upon the sudden cessation of powerful and varied music; at such times we seem to be the subject of a "silence which can be heard."

§ **847**. As in the case of visual sensations, so likewise in the case of auditory sensations the duration of the sensation is longer than that of the action of the stimulus, the auditory sensation lasts after the waves of sound have ceased to fall upon the ear. Hence when two sensations follow each other within a sufficiently short interval, they are fused into one. Since a membrane, thrown into vibrations by a passing sound may continue to vibrate after the sound has ceased, we might perhaps expect that this would be the case with the tympanic membrane, and that hence the interval of fusion would be longer in the case of hearing than in that of vision, for in the latter case we have no corresponding behaviour of any part of the dioptric apparatus. But we have seen (§ 816) that the acoustic arrangements of the tympanum very rapidly damp the tympanic membrane; and, as a matter of fact, the interval in question is decidedly shorter in hearing than in vision. Visual sensations separated by less than $\frac{1}{10}$ sec. may become fused (§ 749); but auditory sensations separated by not more than $\frac{1}{100}$ sec. may remain distinct; if two seconds pendulums be set swinging not quite in accord with each other and made to tick, the tick of the one can be distinguished from that of the other even when they differ in time by not more than $\frac{1}{100}$ sec.

§ **848**. When two notes are sounded at the same time the two sound waves (we may suppose the notes to be pure ones, consisting of a fundamental tone only without partial tones) do not travel as two separate waves, but are compounded, as we have already said, into a single wave, the characters of which will depend on the relative characters of the two constituents. If the two notes have the same period, that is to say are identical, the effect will be simply an increase in amplitude; the compound wave will have its crests higher, and its troughs deeper than those of either of the single waves, but will otherwise be like both of them. If two tuning-forks of exactly the same pitch be struck, the sensation which we experience is the same as that which we experience from either of them alone, only more intense; the sound is louder.

If however the two tuning-forks are not of the same pitch, but so related that the period of vibration of the one is not an exact multiple of that of the other, the sensation which we experience when the two sound together has certain marked features. We hear a sound which is the effect on our ear of the compound wave formed out of the two waves; but the sound is not uniform in intensity. As we listen the sound is heard now to grow louder and then to grow fainter or even to die away, but soon to revive again, and once more to fall away, thus rising and falling at regular intervals, the rhythmic change being either from sound to actual silence or from a louder sound to a fainter one. Such variations of intensity are due to the fact that, owing to the difference of pitch, the vibratory impulses of the two sounds do not exactly correspond in time. Since the vibration period, the time during which a particle is making an excursion, moving a certain distance in one direction and then returning, is shorter in one sound than in the other, it is obvious that the vibrations belonging to one sound will so to speak get ahead of those belonging to the other; hence a time will come when, while the impulse of one sound is tending to drive a particle in one direction, say forwards, the impulse of the other sound is tending to drive the same particle in the other direction, backwards. The result is that the particle will not move, or will not move so much as if it were subject to one impulse only, still less to both impulses acting in the same direction; the vibrations of the particle will be stopped or lessened, and the sensation of sound to which its vibrations are giving rise will be wanting or diminished; the one sound has more or less completely neutralized or "interfered" with the other, the crest of the wave of one sound has more or less coincided with the trough of the wave of the other sound. Conversely at another time, the two impulses will be acting in the same direction on the same particle, the movements of the particle will be intensified, and the sound will be augmented. And the one condition will pass gradually into the other. The repetitions of increased intensity thus brought about are spoken of as *beats*.

The length of the interval at which the beats recur will depend on the difference of period of the two sounds in relation to the actual period or pitch of each. It may be stated generally that the number of beats in a second is equal to the difference between the number of vibrations per second of the two sounds; thus two very low pitched tuning-forks, vibrating respectively at 64 and 72 a second, will give 8 beats a second, and two very high pitched tuning-forks, vibrating respectively at 4224 and 4752 a second will give 528 beats a second; but in this respect there are complications to be presently considered.

Beats are produced when the periods of the coincident sounds are not exact multiples of each other. When the periods are exact multiples no beats occur; two tuning-forks, for instance, the period of one of which is exactly double that of the other, give rise to no beats when sounding together; and so in other instances.

By beats then a continuous musical sound may be broken up into a series of discontinuous sounds. When the beats are repeated a few times only in a second the discontinuous sounds give rise to discontinuous sensations; we hear the separate beats. But if the beats are repeated sufficiently rapidly the successive sensations are fused into one, we cease to hear the beats as such, though we have other evidence that the beats continue to be produced. Just as a series of simple vibrations when repeated sufficiently rapidly, say 40 times a second, gives rise, by summation, to a single musical sound, to a tone, so a series of groups of vibrations, each group corresponding to the interval between two beats, gives rise when the groups follow each other rapidly, by a similar summation, to a continuous sensation.

The rapidity, however, with which beats must be repeated in order to give rise to a continuous sensation, is different from that with which single vibrations must be repeated in order to give rise to a musical sound. Beats repeated 30 or 40 times a second are readily distinguished as such; it is not until they reach a rapidity of repetition of about 132 a second that they cease to be distinctly recognized. Before they disappear or as they disappear, at the time when they can no longer be recognized as separate beats, but have not as yet become fused into a completely continuous sensation, they give to the sound which they accompany a peculiar quality, a particular roughness and harshness. This quality if excessive is disagreeable to the ear; we speak of it as dissonance.

When two notes are sounded at the same time, it has also been found that certain other tones may be heard which are known as "combination" tones. Two kinds of these have further been distinguished as "difference" and "summation" tones. The former are tones which would be produced by vibrations of the same frequency as the difference between the two primary tones; thus, two tones depending respectively on 200 and 250 vibrations per second will give a difference tone corresponding to 50 vibrations per second. Further, the higher tone of 250 vibrations will give with the first overtone of the lower (200) tone, viz. with 400 vibrations, a second difference tone of 150 vibrations. The vibrations of the same tones, 200 and 250, added together make 450 vibrations, and a tone, a "summation" tone corresponding to this number of vibrations can actually be heard, but there is reason to believe that it is rather a difference tone between one of the primary tones and one of the higher overtones. There seems to be little doubt that combination tones are not objective, that they have no counterpart in the complex wave as it reaches the membrana tympani. They seem to be due to some peculiarity of the physiological mechanism of the ear.

From what has been said it is obvious that when a piece of music is played on an instrument, and still more when it is played, as in a concert, on several instruments of different kinds, the disturbance in the air, and the consequent vibrations of the tympanic membrane and of the perilymph, are in the highest degree complex. If the disturbance has certain characters, the sound gives us pleasure, if other characters, we regard the sound as disagreeable; and it is found that the disagreeable features of music are associated with the presence of beats, and still more with the presence of that ill-defined roughness which, as we said just now, is the characteristic of beats when, through rapidity of repetition, they are about to disappear. At the same time there are reasons for thinking that it is the prominence rather than the mere presence of this element which offends the ear, that the element is a necessary ingredient of effective music, and that even the very quality of a musical sound is dependent in part on a certain minute admixture of vibrations disagreeing in period with the fundamental tone and with the regular partial tones. But this is a matter into which we cannot enter here; we have referred to it because it illustrates the extreme complexity of the processes which underlie our sensations of sound.

## SEC. 4. ON THE DEVELOPMENT OF AUDITORY IMPULSES.

§ **849**. We may now turn for a little while to the obscure question, How the vibrations of the perilymph give rise to auditory impulses and so to auditory sensations.

In speaking of the ossicles (§ 817) we gave reasons for thinking that the vibrations of the tympanic membrane are carried onward by the chain of ossicles swinging as a whole, and not conveyed through the chain from molecule to molecule. A similar argument may be applied to the perilymph. The dimensions of the whole labyrinth compared with the length of the waves of sound are so minute that molecular vibrations may be neglected. Moreover the walls of the labyrinth may, as a whole, be regarded as absolutely rigid, so that, the perilymph being incompressible, each blow given at the fenestra ovalis is transmitted instantaneously through the whole mass of perilymph; the fluid driven in by the inward thrust of the stapes has to find room for itself elsewhere, and that room is furnished by the outward bulge of the membrane of the fenestra rotunda, for we may neglect other means of escape such as the lymph spaces around the endolymphatic duct, the nerves, and the blood vessels. Hence at each movement of the stapes the whole mass of the perilymph swings bodily, the membrane of fenestra rotunda moving outwards and inwards at the same instant that the stapes moves inwards and outwards; and each such mass-vibration of the perilymph repeats the characters of the vibration of the ossicles and tympanic membrane, of which it is the continuation.

As they sweep over the vestibule, these vibrations are communicated through the walls of the enclosed membranous labyrinth to the endolymph. The vibrations of the endolymph, or of the walls themselves, affect in some way or other the auditory epithelium of the three cristæ and the two maculæ.

The vibrations also travel from the vestibule into the scala vestibuli of the cochlea, ascending the spiral from below upwards. As they ascend they are transmitted across the membrane of Reissner, the endolymph of the canalis cochlearis, and the basilar membrane to the scala tympani, and so reach the fenestra rotunda.

The bulk of the vibrations ascending the scala vestibuli thus reach the scala tympani by crossing the canalis cochlearis, and in so crossing affect in some way or other the auditory epithelium of the organ of Corti; it is probably only a remnant which at the summit of the spiral passes directly from the one scala to the other.

The features of the basilar membrane point to its being readily thrown into vibrations, and we may conclude that the vibrations started at the fenestra ovalis and transmitted from the scala vestibuli to the scala tympani throw the basilar membrane into corresponding vibrations.

In the cochlea the connection of the fibres of the auditory nerve seems to be exclusively limited to the hair-cells, inner and outer; and we may conclude that these hair-cells are in some way or other concerned in the development of auditory impulses. This view is supported by the analogy of vision; for we have seen reason to think that visual impulses begin in the rods and cones, which like the hair-cells are modified epithelium cells, and we shall presently find that modified epithelium cells also play an essential or important part in the development of sensations other than those of vision and hearing.

Accepting provisionally the view (we will return to the point later on), that the vestibular nerve also conveys auditory impulses started in the cristæ and maculæ, and leaning on the analogy of the cochlea in which as we have just said it seems clear that the hair-cells alone are connected with the auditory fibres, we may conclude, in spite of the divergence of opinion as to the results of histological inquiry, that in the cristæ and maculæ it is the hair-cells also which in some way or other originate auditory impulses. The relatively long hairs of the cristæ, exceedingly long in some of the lower animals, seem specially fitted to take up the vibrations of the endolymph, that is to say, to be thrown into bodily (transversal) vibrations and to communicate those vibrations to the substance of the cell which bears them.

It has been observed that, among the auditory hairs of the crustacea, some will vibrate to particular notes; and as we shall see presently, the vibration of particular hairs in response to particular tones might play an important part in the development of auditory sensations. But the auditory hairs of the mammal even in the cristæ are far too much of the same length to permit the supposition that they can act satisfactorily in this way. Moreover even such fitness as may seem to be present in the cristæ is less conspicuous in the shorter hairs of the maculæ, and vanishes wholly in the case of the peculiar short rods of the hair-cells of the cochlea; we can hardly imagine that the latter vibrate bodily, and even in the maculæ and cristæ the hairs, consisting as they do of fine filaments tending to cohere together, seem imperfect instruments for vibratory purposes. On the other hand in the case both of the cochlea, the maculæ and the cristæ, the hairs of the hair-cells have close relations with structures which have the aspect of being 'damping' organs, namely the tectorial membrane over the organ of Corti, and the otolith membrane over the macula, to which we may add the cupula over the crista. It has indeed been suggested that the otoliths may serve as exciting adjuvants of the vibrations of the fluid endolymph, may act as it were as minute hammers enforcing the blows of the fluid; but this is negatived by observations on the auditory organs of certain molluscs. In these animals the organ of hearing is a closed spherical vesicle, part of the lining of which is furnished by an auditory epithelium of hair-cells with short rod-like hairs, and the rest by ciliated epithelium, the former being alone in connection with a nerve which seems to function as an auditory nerve. Within the vesicle lies a large otolith, and it has been observed that while under ordinary circumstances when sounds of not too great intensity are directed towards the object the otolith is kept away from the auditory hairs, but that when too intense a sound is brought to bear upon the organ, the otolith is driven by the cilia down upon the auditory hairs, and obviously behaves as a damper. We may probably conclude therefore that the membrana tectoria and the otolith membrane act as dampers; but if so the view seems natural that the so-called auditory hairs are useful for conveying the damping action from the damper to the hair-cell, and do not serve to communicate the vibrations of sound from the endolymph to the hair-cell. This would lead us to the conception that both in the organ of Corti and in the macula and crista, the vibrations reach the bodies of the hair-cells in some other manner, not by means of the hairs, but by means of the other structures which go to make up the auditory epithelium; and indeed it is much more in respect to the general arrangements of the auditory epithelium than to the special characters of the hair-cells that the organ of Corti, which we must certainly regard as the chief auditory mechanism, is so much more highly differentiated than the macula or crista. The hair-cells of the cochlea and of the vestibule are exceedingly alike; but very different is the organ of Corti, with its basilar membrane, reticulate membrane, rods of Corti, and rod cells specialized into cells of Deiters, from the simple macula or crista, which contain besides the hair-cells nothing except the relatively plain rod-cells. We can hardly resist the conclusion that the structures just mentioned play an important part in bringing the vibrations to bear on the hair-cells. But what that part is remains for the present mere subject of speculation.

§ **850**. A complex sound, consisting of vibrations of more than one period, travels as we have said not as a group of discrete waves, each corresponding to a vibration of a particular period, but as a complex wave in which the simple waves are compounded into one; and the vibrations of the tympanic membrane, followed by the vibrations of the perilymph, have the same composite character. When for instance a note is sung, or sounded on a musical instrument, the air in the external auditory passage is not the subject of one set of waves corresponding to the fundamental tone, and of other sets corresponding to the several partial tones, but vibrates in the pattern of one composite wave; the tympanic membrane executes one complex vibration, and a corresponding single complex vibration excites the auditory epithelium. And this holds good not for a single sound only but for a mixture of sounds. We can in a clumsy way take a graphic record of the vibrations of a dead tympanic membrane, by attaching a marker to the stapes; could we take an adequate record of the movements of the living tympanum of one of the audience at a concert, we should obtain a curve, a phonogram, which though a single curve only would be on the one hand a record of the multitudinous vibrations of the concert, and on the other hand a picture of the actual blows with which the perilymph had struck the auditory epithelium.

Now, whatever be the exact nature of the process by which the vibrations of the perilymph give rise to auditory impulses, we may consider it as probable that, in giving rise to those impulses, the complex vibration is analysed again into its constituent simple vibrations, that the vibrations start afresh so to speak in the auditory epithelium, marshalled in the same array as that in which they started from the sounding instruments, as if the auditory epithelium itself constituted the band playing the music. And indeed that something of this kind does take place is indicated by the fact that an adequately sensitive ear can in a musical sound detect one or more of the partial tones as distinct from the fundamental tone, or still more easily can in a mixed concert detect the several notes of the several instruments, though, as we have just said in the movements of the tympanic membrane, all the constituent factors are merged into one complex sweep. We may conclude then that we possess some means of analysing the composite waves of sound which sweep through the perilymph, and of sorting out their constituent vibrations.

There is at hand a simple and easy physical method of analysing composite sounds. If a person standing before an open pianoforte, the loud pedal being held down, sings out any note, it will be observed that a number of the strings of the pianoforte will be thrown into vibration, and on examination it will be found that those strings which are thus set going correspond in pitch to the fundamental tone and to the several partial tones of the note sung. The note sung reaches the strings as a complex wave, but the strings are able to analyse the wave into its constituent vibrations, each string taking up those vibrations and those vibrations only which belong to the tone given forth by itself when struck. If we suppose that each terminal fibril or each group of fibrils of the auditory nerve is connected with a terminal organ so far like a pianoforte-string that it will readily vibrate in response to a series of vibrating impulses of a given period and to none other, and that we possess a number of such terminal organs sufficient for the analysis of all the sounds which we can analyse, and that each terminal organ so affected by particular vibrations gives rise to a sensory impulse and thus supplies the basis for a sensation of a distinct character—if we suppose these organs to exist, our appreciation of sounds is in part explained.

When the rods of Corti were first discovered, it was thought that they were specially connected with the nerve-fibres, and served mechanically to stimulate the fibrils passing along their limbs, by striking them after the fashion of minute hammers. Since these rods, to whose striking resemblance to the keys of a pianoforte we have already called attention, are arranged in a long series the members of which vary regularly in the length and in the span of their arch, from the bottom to the top of the spiral, it was supposed that each pair would vibrate in response to a particular tone, and hence that the whole series served for the analysis of sound.

But this view proved untenable. Whatever purpose they serve, the rods of Corti produce their effect, not by acting directly on nerve fibrils, but by contributing in some way or other to the play of the hair-cells; and, whatever be the way in which they intervene, they do not vary in length and arrangement along the spiral to such an extent as the above view demands. Moreover, they are wholly absent from the rudimentary cochlea of birds, though these creatures very clearly can appreciate musical sounds. This last fact proves indubitably that the rods in question are not absolutely essential for the recognition of tones, since it is in the highest degree improbable that birds are able to recognize tones in some manner absolutely different from that employed by mammals.

In the face of these difficulties it has been suggested that the basilar membrane, which is present in birds as well as in mammals, and which, being tense radially but loose longitudinally, *i.e.* along the spiral of the cochlea, may be considered as consisting of a number of parallel radial strings, each capable of independent vibrations, is the sought-for organ of analysis; for it may be shewn mathematically that a membrane so stretched in one direction only is capable of vibrating in such a manner. And the radial dimensions of the basilar membrane increasing as they do upwards from the bottom of the spiral to near the top give a much greater range of difference than do the rods of Corti. According to this view, when a composite vibration sweeps along the cochlea it throws into sympathetic vibrations those small portions and those portions only of the basilar membrane, the vibrations of which correspond to the single vibrations of which the composite vibration is made up; and the vibrations in turn so affect the overlying structures, that auditory impulses are generated in particular groups of fibrils of the auditory nerve. These auditory impulses reaching the brain give rise to a corresponding sensation of a particular sound.

But the dimensions of even the basilar membrane do not seem wholly adequate for the purpose; since the latest measurements shew that in man its range is very limited. If we take the whole width of the membrane, the range is from ·21 mm. at the base to ·36 mm. at the top, though if we take the specially modified part reaching (§ 831) from the outer feet of the rods to the spiral ligament, we get a wider range, namely, from ·075 mm. at the base to ·126 mm. at the top. These numbers apply to the average measurements in the three whorls of the cochlea; the individual fibres from top to bottom would give a still wider range. On the other hand the estimated number of radial fibres of the membrane is very large, 24,000; and even if we suppose that several fibres always vibrate together, this would still leave some thousands of groups of strings, each group acting as an analyser. The observations on the occurrence of defects in the appreciation of tones in limited regions of the scale (§ 842) are readily explicable on this view. It has been found that the regions of deafness are sharply marked off, and this accords well with the idea that, by disease, certain groups of fibres of the basilar membrane have been put out of function.

Another view which has been advanced is that the whole basilar membrane is thrown into sympathetic vibration with nodal points at intervals from one another depending on the character of the sound. In this case a complex vibration would not pick out certain fibres of the basilar membrane and leave the others unaffected, but the membrane would be thrown into vibrations along its whole length with the exception of the fibres at the nodal points. Those fibres midway between each pair of nodal points would vibrate most strongly, while the fibres on either side of them would present vibrations of gradually decreasing amplitude towards each nodal point. In the case of vibrations of great frequency the nodal points would be near one another; in the case of slow vibrations they would be widely separated. It has been stated in favour of this view that when a part of the cochlea has been removed in dogs, the chief defect which seems to follow is the diminution or loss of appreciation of tones of low pitch, and the defect is the same whatever be the part of the cochlea removed. The partial removal interferes with slow vibrations having widely separated nodal points, but not with those vibrations in which the nodal points are near together.

If each of two coincident vibrations picks out individual fibres of the basilar membrane, it is difficult to understand how combination tones can arise, but the occurrence of these tones becomes more intelligible if the two kind of vibrations, affecting the whole membrane, are superposed.

A suggestion has also been made that the basilar membrane vibrates as a whole and that what is transmitted along the auditory nerve to the cerebrum corresponds to the complex vibration of that membrane in all its complexity, much in the same way that a complex vibration is transmitted along a single wire from one plate of a telephone to another. According to this view no analysing mechanism is present in the cochlea; the nerve vibrations which reach the cerebrum are supposed to correspond in frequency and amplitude with those of the external stimulus; the analysis takes place in some part or other of the brain.

In the present state of our knowledge the whole matter must be left as uncertain. Even if the basilar membrane acts in one of the ways suggested, the other structures in the auditory epithelium present problems as yet insoluble. The true function of the rods of Corti and of the reticulate membrane of which these form a part, of the cells of Deiters, of the inner hair-cells as distinguished from the outer hair-cells, as well as the reason there are four rows of the latter (whereby probably the effect of the vibrations of a group of the basilar fibres is increased) and only one of the former, all these are as yet merely questions which cannot be answered.

§ **851.** Even admitting that, in some way or another, sets of vibrations or, to use a more general term, sets of molecular movements are started in the auditory epithelium, in more or less complete correspondence with the sets of vibrations which originate from the musical instrument or other sounding body, and admitting further that each set of such molecular movements in the auditory epithelium starts a particular nervous impulse in a fibril or in a set of fibrils of the auditory nerve, we are very far from having solved the problem of hearing.

It must be borne in mind that making the fullest allowance for the assistance afforded us by the organ of Corti, the appreciation of any sound is ultimately a psychical act. The analysis of the vibrations by help of the basilar membrane or otherwise is simply preliminary to a synthesis of the auditory impulses so generated into a complex sensation. We do not receive a distinct series of specific auditory impulses resulting in a specific sensation for every possible variation in the wave-length of sonorous vibrations any more than we receive a distinct series of specific visual impulses for every possible wave-length of luminous vibrations. In each case we have probably a number of primary sensations, from the various mingling of which, in different proportions, our varied complex sensations arise; but there is this difference between the eye and the ear that whereas in the former the number of primary sensations appears to be limited to three or to six, in the latter the number is probably very large; no suggestion has even been made as to what the exact number may be. Our appreciation of a sound is at bottom an appreciation of the combined effect produced by the relative intensities to which the primary auditory sensations are, with the help of the organ of Corti, excited by the sound. The appreciation and the subjective analysis of sounds is ultimately a psychical process; and though there are individual differences in the structural finish and physical capabilities of the auditory epithelium as of other parts of the ear, the differences in the psychical or at least cerebral powers of individuals are far greater; and when we speak of a musical ear we really mean a musical mind or a musical brain.

§ **852.** If the organ of Corti, as appears from the above, affords the means by which we appreciate tones, it is evident that by it also we must be able to estimate loudness, for the quality of a musical sound is dependent on the intensity, as well as on the pitch, of the partial tones in relation to the fundamental tone and to each other. And since noise is but confused music, and music more or less orderly noise, the cochlea must be a means of appreciating noises as well as sounds. But if this be so, what functions are fulfilled by the vestibular division of the labyrinth ?

We have seen (§ 642) reason to think that the fibres of the vestibular nerve convey afferent impulses which are not auditory in nature in the sense of serving as the basis of sensations of sound, but which affect in a special way the movements of the body. We then discussed the matter exclusively in reference to the cristæ of the semicircular canals; but the view has been extended to the maculæ of the utricle and saccule. It is contended that while the former are affected by movements involving a rotation of the head, the latter are affected by movements in which the head is carried in a straight line, either vertical as when the body rises or falls, or horizontal as when the body progresses forwards or backwards. It is maintained that the utricle and saccule thus share with the ampullæ in providing impulses by which we become aware of the direction and amount of the movements we execute. Indeed it is urged that the true function of the otoliths and otoconia has no connection with hearing, that these act neither as adjuvants to nor as dampers of an auditory mechanism, but by impinging on the so-called auditory hairs in the movements of the head give rise to the impulses of which we are speaking; and arguments in favour of this view are drawn not only from the arrangement of the otoliths in vertebrates, but also from the distribution and behaviour of similar structures in invertebrates. We have further seen (§ 618) that the vestibular nerve, the division of the auditory nerve distributed to the maculæ and cristæ, differs in its characters, in its mode of development, and especially in its central tracts and central endings from the cochlear nerve, the division of the auditory nerve distributed exclusively to the organ of Corti in the cochlea; and it is stated that the vestibule may be injured without any marked effect on hearing. But we are not thereby justified in concluding, as some have done, that the vestibular nerve does not in any way serve as the channel of auditory impulses. Indeed, if it were true as some have urged that fishes which possess no cochlea at all, or the merest trace of one, do really hear, we may conclude that their power of hearing must depend upon their well-developed vestibular labyrinth. And since the structure of the piscine vestibular auditory epithelium is in the main identical with that of birds, reptiles and mammals, it may be argued that this epithelium serves the same purpose in all the several classes. But there seems very little doubt that in the case of nearly all, if not all, fishes there is no evidence of hearing in the strict sense; they respond to vibrations in some cases, but this response takes place just as readily when the labyrinth is removed, and seems to be due only to cutaneous stimulation. On the other hand, if birds and reptiles receive auditory impulses exclusively from the cochlea, and none at all from the vestibule, it is a matter of wonder that the cochlea of the, for the most part, dumb crocodile should appear almost as highly developed as that of the vocal bird.

The whole evidence as to the part played in hearing by the vestibule is very indefinite. As we said above the distinction between noise and music is a quantitative and fluctuating one; indeed the tendency of inquiry seems to shew that the quality or timbre of a sound, and it is this which so largely contributes to the value of a sound as an element of music, is in part dependent on vibrations, which being irregular, that is, having no exact arithmetical relation to the fundamental tone, may be spoken of as noise. We have, however, no definite knowledge as to whether this element of noise depends on confused stimulation of the fibres of the basilar membrane (or other cochlear structure) or whether it is due to the action of some part of the vestibular epithelium. If the latter be the case it would seem that when we are listening to sounds we do not hear this sound with the cochlea and that with the vestibule, but that we hear each sound, whether it be music or noise, with so to speak the whole ear. But if this be so, then the origin and nature of auditory impulses must be still more complex and difficult than appears from the study of the cochlea alone, perplexing as they even then seem.

## SEC. 5. ON AUDITORY PERCEPTIONS AND JUDGMENTS.

§ **853.** In spite of the many and striking differences between the two senses, it is possible to draw several parallels between auditory and visual sensations. When we are the subject of a visual sensation we refer the cause not to changes taking place in the retina, but to some luminous object in the external world. So also, when we are the subject of an auditory sensation we refer the cause not to changes taking place in the internal ear, but to some sounding body outside the ear and in the vast majority of cases to some sounding body outside ourselves. We do not simply experience auditory sensations, we perceive sounds, cf. § 779.

We have seen that in the case of the eye, visual sensations, excited by events taking place in the visual apparatus itself, may be confounded with sensations excited by objects in the external world; and much the same happens with the ear also. The tympanic membrane for instance may be thrown into vibrations not by waves of sound, but by objects coming mechanically into contact with it; particles of the dried secretion of the external auditory passage, the 'wax of the ear,' playing on the tympanic membrane, may give rise to auditory sensations, a 'buzzing' or 'singing in the ears,' which we cannot by the mere psychological examination of the sensations themselves distinguish from auditory sensations excited in the ordinary way by sonorous vibrations reaching us from some sounding body at a distance. And in a general way, we may speak of *entotic* phenomena, corresponding to the entoptic phenomena on which we dwelt (§ 736) in speaking of vision.

Auditory sensations moreover may arise, in the complete quiescence of the tympanic apparatus and perilymph, as the result of changes either in the auditory epithelium or in the central auditory nervous apparatus. We may be subject to *auditory phantoms* or *hallucinations*, corresponding to ocular phantoms or hallucinations, and like them often misleading or distressing. Few persons, moreover, can listen to exciting music or can hear impressive cries without experiencing "recurrent" auditory sensations.

§ **854.** In one important respect the parallel between hearing and sight fails. When we see an object, the rays of light coming from the object excite a particular part of the retinal expansion; and our appreciation of the position which that object holds in space is based on our power of "localizing" retinal changes. The terminal expansion of the auditory nerve however has no such definite relations to the positions in space of objects from whence sounds are proceeding; we have no evidence that any particular part either of the organ of Corti or of the maculæ is alone or specially affected by sounds coming from a particular quarter; and the evidence that sounds affect the three cristæ differently according to the direction of the sound is at least doubtful. Hence we possess no "auditory field" which can be directly compared with the "visual field;" and our conclusions as to the direction in which the sounds which reach our ears have travelled, our judgments as to the position in space of bodies exciting auditory sensations are formed in an indirect manner.

The vast majority of the sounds which we hear reach the auditory epithelium by way of the tympanic membrane and chain of ossicles; even the sounds which are conducted to the ear through the bones and hard parts of the head pass to a large extent by this way (§ 818); in normal hearing the auditory sensations which are generated by vibrations transmitted directly through the bony walls of the labyrinth to the perilymph are probably insignificant. Now it is only in relation to these latter that the disposition in space of the three semicircular canals can possibly have any meaning; the vibrations reaching the perilymph by way of the tympanic membrane, whatever their original direction, have all the same direction when they enter at the fenestra ovalis, and fall in the same way upon the three semicircular canals. We may therefore conclude that the position in space of the three canals in question has nothing to do with our ordinary judgments as to the direction of sounds. In forming those judgments we are assisted mainly by two things.

In the first place a peculiar character of the outwardness which we attribute to our usual auditory sensations, that by which we judge the sound to arise not only outside the internal ear but outside our whole body, seems, in some way, largely dependent on the vibrations which cause the sensation having travelled along the external auditory passage. If the two passages be filled with fluid the hearer refers the sounds which he hears, in spite of their starting at some distance off, not to the external world outside himself, but to the inside of his own head; the sounds appear to him to come, not it may be remarked from the internal ear or any part of it, but from the roof of the mouth, or the top of the skull, or the back of the head. So also if the ear-pieces of a binaural stethoscope be pushed well up into the auditory passages, the sounds heard through the instrument seem to come from the roof of the observer's own mouth.

The difference between such an abnormal mode of hearing and ordinary hearing does not lie in the fact that in the former case the tympanic membrane is not used at all; for even when the external passage is filled with fluid, a layer of air which always adheres to the tympanic membrane permits at least a certain amount of vibration of that membrane; and on the other hand when the sound is actually generated in the roof of the mouth, and rightly judged to be generated there, the tympanic membrane by its vibrations conducts the greater part of the sound to the internal ear. How it is that the passage of the vibrations through the external passage imparts to the sensation this attribute of outwardness is not clear. Indeed certain sounds may be made to lose this particular outwardness, though the external passage be still employed. If two musical sounds of the same pitch be listened to with the two ears separately by means of two telephones, the sound will, under certain conditions, appear to originate somewhere in the head of the observer.

§ **855.** In the second place our appreciation of the particular quarter from which a sound, recognized by help of the external passage to be of outward origin, has travelled is dependent on our using two ears. As our ordinary vision is largely binocular, so our ordinary hearing is, to a still larger extent, *binaural.* In the case of the ear there are no sharp limitations to the range of the organ of either side; through the medium of the air and external auditory passage or of the hard parts of the head a sound which affects one ear affects to a certain extent the other ear also; hence all our hearing is, under ordinary circumstances, binaural. And in some such way as two visual sensations excited in "corresponding parts" of the two retinas are fused into one, so every sound which reaches us is heard not as two sounds, one by one ear and the other by the other, but as one sound by the two ears together.

When the sounding body is on one side of the head, say the right side, the sensations excited through the right internal ear are more powerful than those excited through the left internal ear; we are not distinctly conscious of the difference between the two sensations, the combined effect is a single sensation; but the difference does affect our consciousness in a certain way, and that affection of consciousness serves as a basis for the judgment that the sounding body is somewhere on our right hand. Hence we are able to judge the lateral much more readily than the fore and aft position of a sounding body. If a tuning-fork be held in the median vertical plane over the head, the eyes being shut, though it is easy to recognize it as being in the median plane, it is very difficult to say what is its position in that plane, *i.e.* whether it is more towards the front or back of the head. Hence also a man who is absolutely deaf of one ear has great difficulty in recognizing the direction of sounds.

Further, when we desire to judge particularly as to the direction of a sound, we listen to it, and in the act move the head into the position in which we hear the sound most distinctly. In this way the movements of the head in hearing play a part somewhat analogous to the movements of the eyes in vision.

Even in the case of ourselves, and still more in the case of some animals, the form of the external ear favours the entrance into the meatus, and hence the access to the tympanic membrane, of sounds travelling in a particular direction; this also assists our judgment of the direction of sounds. Hence, by tying back the ears and affixing artificial ears, differing in shape or position from the natural ones, we may make false judgments in this matter.

Moreover, in forming a judgment as to the direction of sounds we appear to be guided by something more than the mere relative intensity of the sounds falling on the two ears. When a complex sound emanates from a body on one side of us, the constituent vibrations do not travel equally and uniformly over and around the head; some are refracted more than others, so that they do not reach the two ears equally; and besides when they reach them are not equally reflected by the two pinnæ. In this way partial tones of different pitch, and this applies especially to high tones, reach the two tympanic membranes in unequal intensities, and the sound of which they form part appears as heard by the one ear of a quality slightly different from that heard by the other ear; this difference of quality, like the difference in mere intensity of the sound as a whole, serves as a basis for recognizing the direction of the sound. Such a difference will be more marked in the complex sounds which we call noises than in purer and more simple musical sounds; and, as a matter of fact, our appreciation of direction is more accurate in the case of noises than of musical sounds. An exception to this rule is met with in the case of the human voice, the direction of which, though it is as a whole a musical sound, can be judged better than even that of a noise; but noises enter largely into the human voice, and besides we are much more practised in relation to it than in relation to any other kind of sound. All our judgments of the direction of sounds are however at the best imperfect.

§ **856**. Our judgment of the *distance* of sounds is even still more limited. A sound whose characters we know appears to us near when it is loud, and far off when it is faint. A blindfold person will be unable to distinguish between the difference of intensity produced on the one hand by a tuning-fork being held before him, first with the broad edge of the fork toward him and then with the narrow edge, and the difference on the other hand caused by the removal of the tuning-fork to a distance. And our judgments in this respect may be false, as is seen in the effects produced by the ventriloquist. We can on the whole better appreciate the distance of noises than of musical sounds, differences of quality as well as of intensity playing the same part in the judgment of distance as of direction; when a sound becomes distant the intensity of the fundamental tone diminishes more rapidly than do those of the higher partial tones, and hence the quality of the sound is affected.

# CHAPTER V.

## TASTE AND SMELL.

### SEC. 1. THE STRUCTURE OF THE OLFACTORY MUCOUS MEMBRANE.

**§ 857.** The organ of smell resembles the organs of sight and hearing in that it consists of a special nerve, ending in a specialized epithelium. The nerve is the olfactory nerve (§ 674) and the epithelium forms part of the mucous membrane which lines the upper region, comprising the upper and middle turbinal bones and the upper third of the septum, of each nasal chamber. This region of the nasal mucous membrane is called the *olfactory mucous membrane*, the remaining lower region being called the *respiratory* mucous membrane, or sometimes the *Schneiderian* membrane. In ordinary breathing the currents of inspired and expired air are mainly limited to the lower respiratory region, the upper region being reached by means of diffusion or of eddies.

The respiratory nasal mucous membrane closely resembles that of the trachea, and consists of a ciliated epithelium, of several layers, resting on a vascular dermis fairly rich in lymphatic elements. Goblet cells are abundant in the epithelium, and numerous small branched mucous or albuminous glands are found in the deeper layers of the dermis. Filaments from the fifth nerve are distributed to this region, but none from the olfactory nerve.

The olfactory mucous membrane is thicker than the respiratory portion, and has to the naked eye a yellowish colour. The thickness is chiefly due to the development in the epithelium of a nuclear layer similar in general appearance to that of a crista or macula acustica; indeed the resemblance between the olfactory epithelium and the auditory epithelium is in many ways striking. A vertical section discloses, very much as in a macula acustica, a layer of cylindrical or columnar cells, the *cylinder cells*, resting on a thick nuclear layer, below which is seen the dermis traversed in various directions by bundles of non-medullated olfactory fibres. And very much as in a macula, the nuclei of the nuclear layer belong to numerous more or less rod shaped or spindle shaped cells, the *rod cells.*

A cylinder cell consists of a cylindrical cell body of granular cell-substance, the upper border of which forms part of the free surface of the epithelium, and the lower part of which, after bearing a more or less ovoid nucleus, becomes narrow and ends in an irregular branched less granular process lost to view in the nuclear layer. Near the confines of the respiratory mucous membrane, these cylinder cells bear, in some cases, cilia; and indeed at the margin of the olfactory membrane, pass into ordinary columnar ciliated cells; but, as a rule, they bear no cilia elsewhere.

A rod cell consists of a spherical nucleus, surrounded with an exceedingly thin layer of cell-substance, which is prolonged peripherally, as a rod-shaped process directed between the cylinder cells and ending between them at the free surface of the epithelium. In the lower animals, amphibia, the free end bears a fine bundle of delicate hairs, which like cilia are capable of movement, though moving in a peculiarly slow, gentle fashion; whether these cilia-like processes are present in mammals is not as yet settled. Besides this peripheral process the cell bears at the other pole of the nucleus a central process directed towards the dermis. This is more delicate than the peripheral process, often appears varicose, and becomes directly continuous with an olfactory nerve-fibre; it is in fact a nervous process. In some rod cells the peripheral process is longer than others, and the nucleus accordingly placed deeper down; some of the nuclei lie close to those of the cylinder cells, others close to or nearly close to the dermis, and some at intermediate levels; in fact the nuclei which make up the thick nuclear layer are the nuclei of rod cells, these greatly exceeding in number the cylinder cells.

An exception to this last statement should be made in favour of the layer of nuclei lying immediately above the dermis. These are oval not spherical nuclei, and the cell bodies are not in the form of rods but more or less irregularly branched. They have been distinguished as *basal cells.*

Among these cylinder, rod, and basal cells which make up the mass of the epithelium, numerous cylinders of flattened cubical cells, surrounding a narrow lumen, pass vertically down from the surface of the epithelium to the dermis. These are the intra-epithelial ducts of small tubular twisted glands, generally albuminous but sometimes mucous in character, which lie in the deeper parts of the dermis, and which more simple and smaller than the corresponding glands in the respiratory nasal membrane, have been called the "glands of Bowman."

The nuclei of the rod cells not only differ in form from those of the cylinder and basal cells, being spherical, while the latter are oval, but also behave in different ways towards various staining and other reagents; with hæmatoxylin and similar staining reagents they stain less deeply than do the nuclei of the cylinder cells. They are obviously of a very different nature; and since the nuclei of the cylinder and basal cells behave towards reagents very much in the same way as do the nuclei of the cells of the gland ducts, and indeed of the cells in the respiratory portion of the membrane, we may speak of the nuclei of the rod cells as possessing specialized characters. The cell-substance of the rod cells is also of a different nature, more specialized than that of the cylinder and basal cells. The yellowish tint of the olfactory membrane is due to pigment deposited chiefly in the epithelium.

§ **858.** The connective tissue, vascular and lymphatic constituents of the dermis present no special characters; no cushion of modified connective tissue like that seen in the auditory crista or macula is present. The special feature of the dermis is the presence of bundles of fibres of the olfactory nerve arranged in more or less plexiform manner.

An olfactory nerve-fibre is a non-medullated nerve-fibre consisting of an axis-cylinder, whose fibrillation is at times conspicuous, surrounded by a sheath or neurilemma, and bearing oval nuclei at intervals. Fibres of this kind are bound up by delicate connective tissue into small bundles, and these by coarser connective tissue into larger bundles. From the olfactory bulb (§ 674) numerous large bundles are given off which, piercing the cribriform plate of the ethmoid bone, run in a plexiform manner in the walls of the nasal chamber in the olfactory region, giving rise to bundles which become successively finer.

From the bundles lying in the dermis immediately below the epithelium, fibres pass into the epithelium itself, the demarcation between epithelium and dermis being in the olfactory region not very sharply defined. These fibres pass into the nuclear layer and then become continuous with the central processes of the rod cells, but have, so far as we know, no connection with the cylinder cells. We may conclude therefore that the rod cells are primarily concerned in the development of olfactory nervous impulses. It does not, however, necessarily follow that the cylinder cell is merely a "supporting" cell in the sense that it simply affords a mechanical support to adjoining rod cells. It is possible that the cylinder cell has some intimate relations, not of a purely mechanical kind, to the wellbeing and activity of the rod cell.

Filaments from the fifth nerve are also distributed to the olfactory as well as to the non-olfactory region of the membrane.

## SEC. 2. OLFACTORY SENSATIONS.

§ **859**. Particles of odoriferous matters present in the inspired air, passing through the lower nasal chambers, diffuse into the upper nasal chambers, and falling on the olfactory epithelium produce sensory impulses which, ascending to the brain, give rise to sensations of smell. We may assume that the sensory impulses are originated by the contact of the odoriferous particles with the free endings of the rod cells; but we are wholly in the dark as to the manner in which the contact of the particles with the cells brings about the molecular changes constituting a nervous impulse. We cannot even say whether we ought to speak of the first step by which the contact of the particle begins the series of changes as a chemical or as a physical process.

In nearly all cases the odoriferous particles are conveyed to the membrane in a gaseous medium, namely, the atmosphere; but before they can gain access to the cells they must become dissolved or at least suspended in fluid; for the whole olfactory membrane is kept moist by a layer of fluid, the secretion of the glands described above, and the odoriferous particles must pass into this layer of fluid before they can gain access to the cells. Indeed, the proper condition of this layer of fluid is one of the essential conditions of the exercise of the sense. If on the one hand the membrane be too dry, or if on the other hand the secretion be too abundant or altered in quality, the power of smelling is diminished or even wholly suspended. It is a matter of common experience that a nasal catarrh interferes with smell. When the nostril is filled with rose-water the odour of roses is not perceived; and simply filling the nostrils with distilled water suspends for a time all smell, the sense gradually returning after the water has been removed; the water apparently acts injuriously on the delicate olfactory cells. If instead of using rose-water, the rose scent be dissolved in "normal saline solution" which (§ 14) more closely resembles the natural secretion, the cells can perform their function, and the scent is perceived. These experiments are not, however, very satisfactory, for it is impossible to say with certainty in any case that the rose-water has penetrated to all parts of the nasal chambers and the scent may have been perceived owing to diffusion to a part which has escaped. There is, however, no doubt that the glands of the olfactory membrane form an important subsidiary apparatus for the development of olfactory sensations.

The other subsidiary apparatus of smell is exceedingly meagre. By the forced nasal inspiration, called sniffing, we draw air so forcibly through the nostrils that currents pass up into the upper as well as the lower nasal chambers; and thus a more complete contact of the odoriferous particles with the olfactory membrane than that supplied by mere diffusion is provided for.

§ **860.** We have every reason to think that any stimulus applied to the olfactory cells will produce the sensation of smell; but the proof of this is not absolutely clear; and we have no definite evidence as to what is the result of directly stimulating the fibres of the olfactory nerve. The olfactory membrane however is certainly the only part of the body in which odours as such can give rise to any sensations: and the sensations to which they give rise are always those of smell. The mucous membrane of the nose is however also an instrument for the development of afferent impulses other than the specific olfactory ones. Chemical stimulation of the nasal mucous membrane by pungent substances such as ammonia gives rise to a sensation distinct from that of smell, a sensation which does not afford us the same information concerning the chemical nature of the stimulus, as does a real olfactory sensation, and which is much more allied to the sensations produced by chemical stimulation of other surfaces sensitive to chemical action. This sensation moreover seems to be developed both in the non-olfactory, and in the olfactory regions of the nasal mucous membrane. Individuals who are unable to smell owing to disease or injury of the olfactory nerve may yet recognize substances such as ammonia and ether, and it is probable that these two kinds of sensations, the one produced by odours, the other by pungent substances, thus arising in the olfactory membrane are conveyed by different nerves, the former by the olfactory, the latter by the fifth nerve.

There appears to be a certain connection between the molecular weight of a gas and the presence or absence of odour. Gases of less than a certain molecular weight are odourless. It has been found that some individuals are wholly insensitive to certain odours, and one of the commonest defects of this kind is inability to smell hydrocyanic acid, a compound whose molecular weight lies near the boundary between odourless and odorous gases. It has further been noticed that compounds of elements belonging to the same group under what is known as the "periodic law" have odours with a certain resemblance to one another. These facts are the only guides we have to enable us to connect the characters of an olfactory sensation with the chemical constitution of the body giving rise to it.

The sensation takes some time to develop after the contact of the stimulus with the olfactory membrane, and may last very long. When the stimulus is repeated the sensation very soon dies out: the sensory terminal organs speedily become exhausted. The larger, apparently, the surface of olfactory membrane employed, the more intense the sensation; animals with acute scent have a proportionately large area of olfactory membrane. The greater the quantity of odoriferous material brought to the membrane, the more intense the sensation up to a certain limit; and an olfactometer for measuring olfactory sensations has been constructed, the measurements being given by the size of the superficial area, impregnated with an odoriferous substance, over which the air must pass in order to give rise to a distinct sensation. The limit of increase of sensation however is soon reached, a minute quantity producing the maximum of sensation and further increase giving rise to exhaustion. The minimum quantity of material required to produce an olfactory sensation may be in some cases, as in that of musk, almost immeasurably small.

In ordinary circumstances odoriferous particles reach both nostrils, and we receive two sets of olfactory nervous impulses, one along each olfactory bulb. These however are fused into one sensation; our olfactory sensations are almost exclusively binasal. When two different odours are presented separately to the two nostrils, by means of two tubes for instance, the effect is not always the same. Sometimes an oscillation of sensation similar to that spoken of in binocular vision (§ 800) takes place. At other times the particular result depending on the nature of the odours, one sensation only is felt, the one sensation wholly destroys the other. And we may infer from this that when, as frequently happens, in a mixture of odours we can only recognize one dominant odour, the suppression of the missing sensations is not due to the chemical action of one odour upon another, or to the one odour preventing the other from acting on the olfactory cells; but from a central cerebral obliteration of all the sensations but one.

It is said, further, that two different sensations may wholly neutralize one another under these conditions if their intensities be suitably graduated. This reciprocal neutralization of odours may be regarded as analogous to the neutralization of two colours, such as yellow and blue, when mixed together, but differs from the latter in the absence of any remaining sensation analogous to grey.

It has been found that fatigue to one odour may bring about a condition of insensitiveness, not only to that odour, but to a certain group of odours, the sensitiveness to other odours remaining normal. This fact, in conjunction with the results of mixture of smells and the fact of insensitiveness to certain smells in some individuals, has led some to attempt a physiological classification of odours. It has even been suggested that our multifarious olfactory sensations may be reduced to a smaller number of primary sensations mixed in various proportions, but the facts are at present too scanty to allow any positive conclusions on this question.

§ **861**. As in the cases of the previous senses, we project our olfactory sensations into the external world; the smell appears to be not in our nose, but somewhere outside us. We can judge of the position of the odour however even less definitely than we can of that of a sound. Our chief guide seems to be that we by turning the head ascertain in which direction we experience the strongest sensations.

The sense of smell seems to play a far more important part in the lives of the lower animals than it does in our own life; and what we now possess is probably the mere remnant of a once powerful mechanism. We may perhaps connect with this on the one hand the fact that, even in ourselves, the olfactory fibres have allotted to them what is virtually a whole segment of the brain, namely the olfactory lobe, and on the other hand the fact that olfactory sensations seem to have an unusually direct path to the inner working of the central nervous system. Mental associations cluster more strongly round sensations of smell than round almost any other impressions we receive from without. And powerful reflex effects are very frequent, many people fainting in consequence of the contact of a few odorous particles with their olfactory cells.

The assertion that the olfactory nerve is the nerve of smell has been disputed. Cases have been recorded of persons who appeared to have possessed the sense of smell, and yet in whom the olfactory lobes were found after death to be absent. Direct experiments on animals however shew that loss of the olfactory lobes entails loss of smell. On the other hand, it is stated that section or injury of the fifth nerve causes a loss of smell though the olfactory nerve remains intact; but in these cases it has not been shewn that the olfactory membrane remains intact, and it is quite possible that, as in the case of the eye, changes may take place in the nasal membrane as the result of the injury to the fifth nerve, sufficient to prevent its performing its usual functions.

## SEC. 3. THE STRUCTURE OF THE ORGANS OF TASTE.

§ **862**. Sensations of taste, like those of sight, hearing, and smell, are brought about by means of special nerve-fibres whose endings are connected with a modified epithelium; but these special nerve-fibres do not form a nerve devoted exclusively to taste as the optic nerve is to sight, the olfactory nerve to smell, and, though less distinctly, the auditory nerve to hearing; they run in company with fibres of other kinds in one or other or both of two cranial nerves, in the glossopharyngeal nerve and in the lingual branch of the fifth nerve. In this respect the sense of taste shews a tendency to a more general distribution similar to that of touch; and in the lower animals this tendency is still more strongly marked. Moreover, though, as we shall see, a modified epithelium, subserving taste, does exist in the lining of the mouth, it is not so clear, as in the case of sight, hearing, and smell, that the development of gustatory sensations is exclusively dependent on this modified epithelium; there are reasons for thinking that taste may be exercised by parts of the mouth where no such distinctly modified epithelium exists.

Although the lining membrane of the mouth is generally spoken of as a "mucous membrane," its histological plan is identical with that of the skin. The epithelium overlying the dermis is a stratified epithelium, consisting of many tiers of cells, in which we may distinguish a lower malpighian layer and an upper corneous layer. One of the chief differences between the epithelium of the mouth and the epidermis of the skin is, that in the former the stratum granulosum and stratum lucidum (§ 434) so characteristic of the latter, are absent, or present in a few places only, being replaced by a layer in which the polygonal prickle cells of the malpighian layer, losing their prickles and becoming flatter, are gradually transformed into the cells of the corneous layer. Another difference is that the uppermost cells of the corneous layer, though transformed into flat scales, still retain a conspicuous nucleus, and are not so wholly corneous as the corresponding scales of the skin. The differences appear to be connected with the fact that the epithelium of the mouth is always soaked in moisture, whereas the epidermis of the skin is as a rule dry.

The dermis, thrown up into numerous conspicuous papillæ, contains a considerable quantity of reticular, or at places, even adenoid tissue, is extremely vascular, plexiform arrangements of the veins being very frequent, and in it in many situations, for instance in the tongue, striated muscular fibres end with branched terminations; numerous small, chiefly albuminous glands are also present, especially in certain regions.

In the tongue, the papillæ, which are for the most part compound, have been divided into three classes; filiform, fungiform, and circumvallate. The two first, which are much the most numerous, differ chiefly in form, the one being more or less pointed, the other having a broad head; both generally bear secondary papillæ. The circumvallate papillæ, few in number, arranged in the form of a V with the apex at the root of the tongue, are distinguished by the fact that the papilla is as it were sunk into the substance of the tongue, so that its base is surrounded by a circular groove like a fort surrounded by its fossa and vallum.

§ **863.** Appearing irregularly and scantily on the fungiform papillæ and then seated sometimes at the sides, sometimes on the top of the papilla, more abundant on the circumvallate papillæ in which they are seated generally on the sides of the papilla, looking into the groove, but sometimes on the opposite wall or vallum, are the structures known as *taste-buds* or "taste-bulbs." These are especially abundant and most easily studied in the aggregations of papillæ, which in some animals, for instance the rabbit, are found at the back of the tongue and are called *papillæ foliatæ.* In the rabbit these are seen by the naked eye as two oval patches, one on each side, placed obliquely at the root of the tongue. Upon examination each patch is found to consist of a number, twenty or so, of folds of the mucous membrane placed side by side like the leaves of a book. In each fold the dermis is raised up into three narrow parallel ridges which in a transverse section appear as three pointed papillæ. The epithelium, which here as elsewhere consists of a malpighian and a corneous layer, is somewhat thin at the sides of the fold, but thicker at the top, where it is even, not following in contour the ridges of the dermis beneath. Hence, in each fold, the two outside ridges of the dermis, which look towards the deep narrow furrows separating each fold from adjacent folds, are covered by a somewhat thin but complete epithelium. And in a transverse section this epithelium is seen to contain a vertical row of oval structures, four or five in number, which reach from the dermis to the surface of the epithelium, each furrow having a row of such structures on each side. These are the taste-buds, having essentially the same structure as those seen in man less regularly distributed on the sides of the circumvallate papillæ, and still less regularly on the fungiform papillæ.

Each taste-bud consists on the outside of an oval hollow structure, which may be compared to an oval nest, the walls of which are formed of epithelial cells arranged thatch-wise. The base of the nest lies bare on the dermis, the top of the nest comes to the level of the surface of the epithelium, and here bears a circumscribed circular hole, or mouth, by means of which the fluids of the mouth can gain access to the inside of the nest. The cells forming the walls are elongated, flattened, fusiform, appropriately curved, nucleated cells, arranged in an imbricate fashion, the outer ones passing somewhat abruptly into the ordinary cells of the malpighian and corneous layers. Those ends of the cells which converge to form the top of the nest are scooped out, or bear distinct perforations, and thus in the one way or the other form the margin of the mouth or pore leading to the inside of the nest. The cell-substance forming the scooped margin or surrounding the perforation seems to be cuticularized so as to secure the patency of the pore.

The cells thus forming the walls of the nest differ from the surrounding ordinary cells chiefly in form; at least they cannot be spoken of as distinctly modified in respect to their actual nature. The interior of the nest however is occupied by cells, which we must regard as specialized sensory cells. These are of two kinds. The one kind, very similar to the rod cells of the olfactory organ, are called *rod cells*; the other kind, analogous to the cylinder cells of the olfactory organ, we may call *subsidiary cells*; they have also been called "cover-cells." The rod cell consists of an elongated oval nucleus placed vertical, at about the level of the middle of the nest. The scanty cell-substance surrounding the nucleus is prolonged peripherally as a rod-shaped, nearly hyaline, somewhat refractive process which reaches up, or projects through the pore of the nest; the cell-substance is also prolonged centrally as a delicate thread-like process, which either branching or unbranched, stretches towards and is lost to view at the dermis.

The subsidiary cell possesses a nucleus which is larger and more rounded than that of the rod cell, and its cell-substance, larger in amount and more granular in appearance than that of the rod cell, has a more or less fusiform shape, the part peripheral to the nucleus ending in a tapering fashion, and the part on the other, central, side of the nucleus becoming branched and lost to view near the dermis.

The axis of the nest is occupied by a group of rod cells, the peripheral processes of which converge in a bunch at the pore of the nest. With these however are interspersed a few subsidiary cells, and the core thus formed is surrounded by a wrapping consisting of subsidiary cells only. Both the rod cells and subsidiary cells differ from the cells forming the wall of the nest not only in form but in chemical nature, and behave very differently from them towards various reagents; they stain with gold chloride for instance very readily, and may with this reagent be prepared deeply stained, while the walls of the nest and the rest of the epithelium are hardly stained at all.

In the dermis underlying the taste-buds, nerve-fibres, derived from the glossopharyngeal nerve, are abundant; they may very readily be seen in preparations of the papillæ foliatæ. Some of these are medullated and others sooner or later lose their medulla; some are distributed to parts other than the taste-buds, but some form at the base of the taste-bud a plexus of non-medullated nerve filaments. From this plexus fibrils ascend into the substance of the bud and there end in fine ramifications round the nuclei of the rod cells. There seems little doubt that they are not, as in the olfactory membrane, directly continuous with the rod cells. The existence of the taste-bud is dependent on its connection with the nerve-fibres. If the glossopharyngeal nerve be divided, and regeneration of the nerve prevented, the rod cells and subsidiary cells degenerate and vanish, and finally the whole taste-bud disappears.

The small albuminous glands occurring as we have said in the mucous membrane of the mouth are especially abundant in the neighbourhood of the taste-buds; they serve to supply fluid for the solution of substances to be tasted, and as we shall presently see such a solution seems to be a necessary condition for the activity of the sensory organs. The dermis in the neighbourhood of the taste-bud is always very vascular, and venous plexuses, assuming almost the form of venous sinuses, are not infrequent; such a venous sinus is conspicuous in the central ridge of a fold of a papilla foliata.

Taste-buds are found in other parts of the mouth besides the hind part of the tongue, where as we have said they occur on the fungiform and circumvallate papillæ. They are found in the soft palate, and in not inconsiderable numbers on the hinder surface of the epiglottis. They are absent or extremely rare in the front part and sides of the tongue. Their distribution in fact appears not to coincide exactly with that of the sense of taste itself; and we may therefore conclude that gustatory nerve-fibres have other terminations besides taste-buds. The only other mode of termination however of which we are at present aware, is that mode by which the nerve-fibres, breaking up into fibrillæ, are lost among the cells of the epithelium without ending distinctly in any specially modified cell; but this mode of termination we shall study more closely in dealing with the sense of touch.

It is obvious that a very complete analogy exists between the taste-buds and the endings of the olfactory nerve. The rod cells of the one closely resemble the rod cells of the other, and the subsidiary cells of the taste-bud are clearly analogous to the cylinder cells of the olfactory mucous membrane; and much that we urged as to the relative values of the rod cells and cylinder cells of the olfactory membrane may be applied to the rod cells and subsidiary cells of the taste-buds. The resemblance is carried still further in the case of the olfactory organ of some of the lower animals. In these the olfactory membrane is not a continuous sheet, but is broken up into patches by the intervention of non-olfactory epithelium, and the isolated patches often take on the form of nests very similar indeed to taste-buds. It is obvious that the senses of taste and smell are closely akin, and in many aquatic animals we probably have to do with structures which subserve a sense not exactly that of smell or of taste as we ourselves experience these sensations, but of something intermediate between the two, or possibly between both of them and the more general sense of touch.

## SEC. 4. GUSTATORY SENSATIONS.

§ **864.** The word taste is frequently used when the word smell ought to be employed. We speak of 'tasting' odoriferous substances, such as an onion, a wine, a savoury dish, and the like, when in reality we only smell them as we hold them in our mouth; this is proved by the fact that the so-called taste of these things is lost when the nose is held, or the nasal membrane rendered inert by a catarrh. If the nose be held and the eyes shut it is very difficult to distinguish in eating between an apple, an onion, and a potato; the three may be recognised by their texture, but not by their "taste." Most of what we call 'flavours' appeal in reality to the sense of smell, not to that of taste.

We also experience by means of the surfaces with which we taste sensations other than those of taste. We feel by means of the mucous membrane of the mouth sensations of the same kind as those which we feel by means of the skin, and which we shall study presently as tactile sensations or sensations of pressure, sensations of heat and of cold; indeed the tactile sensations of the tip of the tongue are remarkably acute. We also experience by means of the mouth sensations of pain and other more or less indefinite sensations which we shall presently speak of as phases of "general" or "common sensibility;" and in this respect the mucous membrane of the mouth is much more sensitive than the skin towards chemical substances; an acid for instance or other corrosive liquid, in such a concentration as when applied to the skin produces a sensation not essentially different from that of mere contact with an innocuous liquid, may when applied to the mouth produce a very painful sensation. Again, when the interrupted current is applied to the tongue we not only feel the contact of the electrodes but experience a peculiar sensation which is probably due to the contractions excited by the current in the muscular fibres of the tongue; we say we "feel the current."

§ **865.** There are however certain sensations quite distinct from those just mentioned and quite independent of smell which we experience when various substances are placed in the mouth; and these, which are the gustatory sensations proper, may be broadly classified into 'bitter,' 'sweet,' 'acid' or 'sour,' and 'salt,' to which some would add 'metallic' and 'alkaline.' The sensation of bitterness, such as that produced by quinine, and the sensation of sweetness, such as that produced by sugar, are very definite and specific sensations; they appear to be of an order different from those of acidity or sourness and of saltness; indeed an acid 'taste' is apt to merge into an affection of general sensibility mentioned above. The 'metallic' and 'alkaline' tastes should perhaps be regarded as due to fusion of taste sensations proper with sensations of touch or of common sensibility, or even of temperature; one of the elements in the 'taste' of peppermint is undoubtedly a sensation of cold.

In the ordinary course of things these sensations are excited by the contact of specific sapid substances with the mucous membrane of the mouth, the substances acting in some way or other, by virtue of their chemical constitution, on the endings of the gustatory fibres. When we taste quinine, the particles of the quinine, we must suppose, set up chemical changes in the cells of the taste-buds or in other parts of the epithelium, and by means of those changes gustatory impulses are started. When we were dealing with smell we found that there was little to enable us to connect the character of a sensation with the chemical constitution of the body giving rise to it. In the case of the two most definite sensations of taste, sweet and bitter, our knowledge is more advanced. Substances which taste sweet or bitter are found always to contain certain definite groups in the molecule, especially the hydroxyl ($OH$) and amido ($NH_2$) groups. Moreover, it seems as if a certain definite balance between positive and negative radicals must exist in order that a substance shall taste sweet, for when such a substance is so altered chemically that this balance is upset, the resulting derivatives are, according to circumstances, either bitter or tasteless. This relation between chemical structure and taste appears to be one of the best instances of correlated chemical constitution and physiological action, and the definiteness of the relation is probably due to the fact that the active substance comes into immediate contact with the physiological mechanism upon which it acts.

Mechanical or electrical stimuli, in the absence of sapid substances, will also give rise to gustatory sensations. When the tongue is smartly tapped, in addition to the sensation of touch or the more or less painful sensation which may be produced, a sensation, which we must call a sensation of taste, is developed and often lasts for some considerable time. If a constant current be applied to the tongue, sensations of taste are developed at the two electrodes, that at the anode differing from that at the kathode, and the exact nature of each being dependent upon the region of the mouth stimulated. It is probable that in this case electrolysis either of the fluids covering the epithelium or of the substance of the epithelial cells themselves generates bodies which act as chemical stimuli; and it is possible that the mechanical disturbance of the cells, when the tongue is tapped, also sets free chemical stimuli. But sensations of taste may be provoked by an interrupted induced current, so feeble as not to be felt as an electric current, and so arranged that the make and break shocks are equalized; in this case there can be little or no electrolysis, and we may infer that the current acts in some way or another on the specific nerve endings. It is somewhat singular that heat when applied to the tongue appears not to produce any sensations of taste.

As we shall presently see, the nerve-fibres concerned in taste belong either to the fifth nerve or to the glossopharyngeal nerve or to both nerves. We saw in dealing with vision that the evidence as to whether direct stimulation of the optic fibres without the intervention of the retinal structures could produce visual sensations was uncertain. We have no satisfactory evidence whatever that direct stimulation of the gustatory fibres along their course in either the above two nerves will produce sensations of taste. As far as the sense of taste is concerned we have no adequate evidence that specific gustatory impulses can be developed in the gustatory fibres apart from changes in the nerve endings. But the evidence is negative only; and the case is one not suited for experiment, since both nerves along their whole course are mixed nerves containing other afferent fibres than those of taste.

§ **866.** It is essential for the development of taste, that the substance to be tasted should be dissolved; hence, the value of the glands, which as we have seen are especially abundant in the neighbourhood of the taste-buds. The effect is also increased by friction; and the tongue and lips may be regarded as a subsidiary apparatus which by their movements assist in bringing the sapid substances into contact with the mucous membrane of the mouth. A substance may give rise to hardly any sensation of taste when simply placed on the extended tongue, and yet excite very distinct sensations when rubbed between the tongue and the soft palate; indeed we generally make use of this movement known as "smacking the lips," when we desire to obtain strong taste sensations. In this act however we not only make use of the most sensitive surfaces and call in the aid of friction, but we also increase the sensation by employing a large area of sensitive surface; for the larger the surface the more intense is the sensation. Movements may also be useful by assisting the entrance of sapid substances into the taste-buds.

The sensation takes some time to develope, and endures for a long time, though this may be in part due to the stimulus remaining in contact with the terminal organs.

A temperature of about 40° is the one most favourable for the production of the sensation. At temperatures much above or below this, taste is much impaired. A weak solution of quinine readily tasted at the normal temperature of the mouth is not tasted if, immediately before, very cold or very hot water be held in the mouth for a little while.

We may experience at the same time coincident taste sensations of different kinds, such for instance as one of bitterness with one of saltness; but in some cases one sensation interferes with the other, as for instance bitterness and sweetness. A taste sensation following upon a previous sensation of a different kind, is frequently influenced by its predecessor, being sometimes augmented, sometimes inhibited.

Though we can hardly be said to project our sensations of taste into the external world, as we do those of sight, hearing and smell, we assign to them no subjective localisation. When we place quinine in our mouth, the resulting sensation of taste gives us no information as to where the quinine is, though we may learn that by concomitant general sensations arising in the buccal mucous membrane. And it must be remembered that all our gustatory sensations are always accompanied by tactile or other sensations. We do not, as in the case of smell, experience the specific sensation alone and apart by itself. And not infrequently, as when substances at once sapid and pungent are placed in the mouth, the general sensation of pungency overcomes and hides the specific gustatory sensation. In the case of acids, it is often difficult to distinguish between the acid taste and the more general effect of the acid on the common sensibility of the buccal membrane of which we spoke above § 864.

There is little doubt that both successive and simultaneous contrast occur in the case of taste. After-tastes have been observed, and it has been found that the application of a sapid substance to one part of the tongue affects taste on other parts of the tongue, but these phenomena are much less definite than in the case of vision.

Though we possess a gustatory apparatus with separate nerves on each side of the mouth all our sensations are single. Nor can we distinguish a pure gustatory sensation developed on one side only from one developed on both sides, if the two are equally intense.

As in the case of the senses previously dealt with, we may experience subjective gustatory sensations, sensations of central origin due to changes in the central sensory organs (§ 676); and these, though originated not by gustatory impulses but by other events, may seem to us identical with those set up in an ordinary way by gustatory impulses reaching the centre along the gustatory fibres.

§ **867**. Sensations of taste are not originated, either by sapid substances or otherwise, equally in all parts of the lining membrane of the mouth. The part in which they are best developed, and always developed if developed at all, is the back of the tongue, in the neighbourhood of the circumvallate papillæ. They are also developed at the tip and along the sides of the tongue, but to a variable extent in different individuals; some persons have very acute and distinct taste sensations in these parts, others little or none at all. On the dorsal surface of the middle of the tongue very feeble taste sensations, if any at all, are developed; they are always absent from the under-surface of the tongue except in some individuals at the tip. Some taste sensations are also developed in the soft palate and front surface of the palatine arches; but these again vary much in distinctness in different individuals. In the cases recorded in which taste remained after the entire extirpation of the tongue including the circumvallate papillæ, the sensations seem to have been chiefly developed in the soft palate. There is also some evidence that taste sensations may be developed on the hinder surface of the epiglottis. It is said that in children sensitiveness to taste is more widely and more uniformly distributed over the mucous membrane of the mouth than in adults.

In individuals who receive sensations from all or several of the various parts above mentioned, it commonly happens that bitter things are most readily appreciated at the back of the tongue and sweet things at the tip; and this distribution may perhaps be considered as the normal one; but individual variations in this respect are met with; many persons taste both bitter and sweet things best at the back of the tongue; and some persons taste bitter things quite distinctly at the tip. The salt taste is said to prevail at the tip and the acid taste at the sides of the tongue; but many persons experience acid and salt tastes in those regions and those regions only in which they experience bitter and sweet tastes.

In addition to these general differences of sensitiveness on different parts of the tongue, it has been found that the fungiform papillæ shew different degrees of sensitiveness to different tastes. If individual papillæ are stimulated, it is found that some are sensitive to all kinds of taste; others to only two or three; others are only sensitive to one kind of taste, even when strong solutions are used, and others again appear to be wholly insensitive to taste. A mixture of sapid substances will give rise to different sensations of taste on different papillæ; a solution of sugar and quinine will taste sweet on one papilla, bitter on another. These facts point very strongly to the existence of special terminal organs for different kinds of taste sensation.

We have already said that bitter and sweet tastes seem to be on a different footing from acid and salt tastes; and we have further evidence that the two former sensations are brought about by means of terminal organs different from those by means of which the two latter are brought about. If some of the leaves of a plant which grows in India and is called *Gymnema sylvestre*, be chewed, or if the mouth be washed with a decoction of the leaves, for some little time afterwards bitter and sweet tastes are lost, neither quinine nor sugar exciting the usual sensations, though acid and salt tastes remain unaffected. We may interpret this result as indicating that the drug in some way or other 'paralyses,' that is to say, suspends the action of, the terminal organs, whatever they may be, by means of which bitter and sweet tastes are developed, but leaves untouched those by which other gustatory sensations are developed. The action of the same drug supports the further conclusion that the terminal organs of bitter tastes are different from those of sweet tastes; since by using an adequately weak dose of the drug the sweet taste may be abolished while the bitter taste remains distinct.

There is little doubt that the distribution of the several kinds of tastes over different regions of the mouth, which we mentioned above, is dependent on the distribution of different kinds of terminal organs; we experience bitter tastes by means of the back of the tongue because the terminal organs of the bitter taste are most abundant in the back of the tongue, those of the sweet taste by the front of the tongue because the terminal organs of the sweet taste are more abundant there; and so on. If a small quantity of a particular bromine derivative of the substance which from its remarkably sweet taste has been called 'saccharine,' be placed carefully on the tip of the tongue, a sweet taste is developed; but if the same substance be carefully placed on the back of the tongue the result is not a sweet but a bitter taste. At least this is the result in the case of those individuals who taste bitter at the back of, and sweet at the tip of, the tongue. From this we may infer that, in such tongues, the specific terminal organs of the sweet taste are more or less completely limited to the front, and those of the bitter taste to the back of the tongue, both sets of terminal organs being of such a nature that while quinine affects the one only and sugar the other only, the substance of which we are speaking is able to affect both of them. In a somewhat similar way certain salts, magnesium sulphate for instance, when applied to the back of the tongue excite a bitterish taste, but when applied to the tip of the tongue excite an acid or a sweetish acid taste.

We said a little while back that a weak interrupted current, so applied as to produce little or no electrolytic effect, was able to develope sensations of taste, varying in kind according to the region of the tongue stimulated. When the electrodes are applied to the tip of the tongue, the more usual result is that though an acid taste is the most prominent, a mixed gustatory sensation is developed, in which a sweet taste may be often recognised as a constituent. In like manner a bitter constituent may be recognised in the sensation developed when the electrodes are placed at the back of the tongue. If the tongue be previously subjected to the influence of *Gymnema*, the taste at the tip is free from all sweetness and that at the back free from all bitterness, the sensations which are then experienced being variously described as simply "metallic," or "salt," or "acid." From this result we may draw the important inference that the interrupted current developes a bitter and a sweet taste by acting in some way or other directly on the specific terminal organs of the two respective tastes, very much in the same manner as do bitter and sweet things. Electrical stimulation, however, of individual fungiform papillæ has not given any very definite result.

We have already said that when an acid, especially a somewhat strong acid, is placed on the tongue or in the mouth, the pure gustatory acid sensation is apt to be confused with the sensation of pungency, the affection of general sensibility which the acid also brings about and which speedily merges into pain. These two sensations may be differentiated by means of cocaine. If the tongue be painted with a weak solution of cocaine, the general sensibility, the groundwork so to speak of pain, is abolished, while the pure gustatory sensations are at first hardly affected at all; a relatively strong acid, which previously made the tongue "smart" so that real gustatory sensations were obscured, now developes a pure "rich" acid taste alone. It is moreover said that cocaine applied to the tongue in increasing strength of solution abolishes the several classes of sensations in the following order: general sensibility and pain, bitter taste, sweet taste, salt taste, acid taste, tactile sensations.

Taking all these facts into consideration, we are led to the conclusion that the development of the several kinds of gustatory sensations depends on the presence of specific terminal organs in the surfaces by means of which we taste. There appear to be distinct terminal organs for bitter tastes, for sweet tastes, for acid tastes, for salt tastes, and possibly for other tastes, all differing from the terminal organs for tactile sensations, and from the structures, whatever they may be, which are concerned in general sensibility. But beyond this it is very difficult to say anything decisive. From the fact that sensations of taste are, as a whole, most constant and most acute at the back of the tongue, in the neighbourhood of the circumvallate papillæ in which taste-buds are present, we may infer that the name taste-bud has been wisely chosen. It is unfortunate that the taste-buds of the circumvallate papillæ cannot, like the fungiform papillæ, be directly stimulated. Only some fungiform papillæ contain taste-buds, but we have at present no evidence to shew that these papillæ are more sensitive to taste than others which do not contain taste-buds. It is said that taste-buds are absent from the tip of the tongue where taste sensations are undoubtedly developed; and if this is true we must conclude that gustatory sensations may originate by the help of some kind of nerve ending other than that of taste-buds. It might be suggested that some tastes are developed by means of taste-buds and other tastes by means of other endings; but there is no satisfactory evidence of this.

§ **868.** The question which nerve or nerves subserve taste and what is the course of the gustatory fibres is one which presents great difficulties. The front surface of the tongue is supplied by the lingual or gustatory branch of the fifth nerve, the hind surface by the glossopharyngeal nerve, which nerve also supplies the soft palate, though a branch (palatine) of the fifth nerve goes there also. The nerves traced to the taste-buds in the papillæ foliatæ and circumvallatæ belong to the glossopharyngeal nerve, and it can hardly be doubted that gustatory fibres run in the branches of that nerve which go to the back of the tongue. On the other hand, in the cases in which sensations are distinctly developed in the tip of the tongue we must infer that gustatory fibres run in the lingual branch of the fifth, since no glossopharyngeal fibres are distributed to this part of the tongue.

But it by no means follows from this that gustatory fibres pass straight both up the trunk of the glossopharyngeal nerve and up the trunk of the fifth nerve to their respective nuclei in the bulb.

On the one hand there is a good deal of evidence to shew a connection between sensations of taste and the chorda tympani nerve. Cases have occurred in which disease of the ear, involving destruction of the chorda tympani within the tympanum, has been followed by loss of taste in the tongue on the same side; and stimulation of the chorda tympani within the tympanum has been known to give rise to sensations of taste. Neither of these results is conclusive. The chorda tympani contains afferent fibres which have a remarkable effect on the nutritive processes of the tongue, and the loss of taste due to destruction of the chorda might be due to disordered nutrition of the tongue, and so be analogous to the loss of smell which may follow injury of the fifth nerve. Again, where stimulation of the chorda within the tympanum produces sensations of taste, these may be due to efferent impulses producing changes in the tongue, which in turn give rise to sensations of taste reaching the brain by other channels than the chorda itself; we have no satisfactory evidence that direct stimulation of the central stump of a divided chorda will give rise to sensations of taste. The connection between the chorda and taste, however, may be of a more real kind.

On the other hand we must bear in mind how varied and complex are the junctions in the skull between the fifth nerve, the seventh nerve, and the glossopharyngeal nerve, by way of the Vidian nerve, the petrosal nerves, the tympanic plexus, Jacobson's nerve, and the otic and sphenopalatine ganglia. And it seems possible to suppose that fibres leaving the brain by the fifth nerve might find their way not directly to the lingual branch but by a roundabout way through the chorda tympani, and that at the same time other fibres from the same fifth nerve might ultimately join the glossopharyngeal nerve. There are no cases on record in which disease of the glossopharyngeal nerve within the cranial cavity has led to distinct loss of taste; but cases have been recorded in which disease of the fifth nerve within the cranial cavity, and as far as could be ascertained limited to the fifth nerve, has led to an entire loss of taste over the whole of one side of the tongue, both back and tip. Such cases lead to the at least provisional conclusion that the gustatory fibres are fibres belonging to the fifth, though they may reach the tongue partly by way of the glossopharyngeal, partly by way of the chorda tympani.

# CHAPTER VI.

# ON CUTANEOUS AND SOME OTHER SENSATIONS.

## SEC. 1. THE NERVE ENDINGS OF THE SKIN.

§ **869.** WE may speak of all the sensations which we derive from the skin as "cutaneous sensations;" we shall later on discuss their various kinds. The afferent nerves of the skin, those which appear to serve as the channels for impulses giving rise to cutaneous sensations, appear to end in two main ways. In the first place nerve-fibres given off from a plexus of medullated fibres lying in the dermis immediately below the epidermis pass upward with loss of their medulla into the epidermis, and there, dividing into delicate nerve fibrils, come into connection with, or are lost to view between the epidermic cells. In the second place, nerve-fibres still retaining their medulla and for the most part running singly, end in the dermis at a variable distance below the epidermis in special structures made up of modifications of the neurilemma, or other wrappings of the nerve-fibre, associated more or less distinctly with cellular elements. We will consider the latter kind of ending first. In man the endings of this kind are two: the *end-bulbs* of limited, and the *touch-corpuscles* of much more general distribution. To these we must add the *Pacinian corpuscles,* which however are found not in the dermis proper, but in the subcutaneous connective tissue, and which cannot be considered as distinctly cutaneous organs, since they also occur far away from the surface of the body, in connection with joints and the periosteum of bones, and even with internal organs. They can hardly be considered as cutaneous organs, but they cannot be left unnoticed. In various animals we meet with other forms of nerve endings, the structure of which throws light on that of the kinds just mentioned.

The *end-bulbs* are found not in the skin generally but in certain situations only, namely, the conjunctiva and the lips, and a special form occurs in the sensitive surfaces of the genital organs. They are not confined to the outer surface of the body, but are found also in mucous membranes, in the tongue and palate, in the rectum and elsewhere. Similar bodies are also found in the synovial membranes of joints.

The end-bulbs in man are small rounded or oval bodies, 30 $\mu$ to 100 $\mu$ in diameter, consisting of a capsule of connective tissue enclosing a core of peculiar material. The capsule is indistinctly fibrillated, and bears nuclei which are sometimes so arranged as to indicate an outer capsule with nuclei placed lengthwise to the longer axis of the bulb, and an inner capsule with nuclei placed crosswise. The core consists of a homogeneous ground-substance in which are imbedded granules, or in some cases nuclei; in some instances the core appears to be made up of small nucleated cells. A medullated fibre, with its neurilemma and sheath of Henle, approaches the end-bulb, and frequently becoming much coiled close to the bulb, plunges into the bulb at its base or side. The sheath of Henle, and perhaps the neurilemma also, becomes continuous with the capsule; the axis cylinder covered with medulla passes into the core, and here, frequently coiling about and at times dividing, loses the medulla, and ends in the midst of the core in a blunt, slightly swollen end, or when it divides, in more than one such knob. Sometimes more fibres than one end in the same end-bulb. The marked feature of an end-bulb is a special development of the connective tissue wrappings of a nerve-fibre, in the midst of which the axis cylinder, with or without previous division, ends abruptly.

**§ 870.** *Pacinian corpuscles.* Though these are relatively large bodies, often more than a millimeter in length and easily seen by the naked eye, their general plan of structure is similar to that of an end-bulb; they may be regarded as very large highly developed end-bulbs.

The axis of the Pacinian corpuscle is furnished by a core, cylindrical, or rather an elongated oval in form, resembling that of an end-bulb in that it consists of a homogeneous ground-substance to which occur granules or small nuclei; in structures very similar to Pacinian bodies occurring in the beaks of some birds (duck), called "Herbst's corpuscles," the core is distinctly composed of nucleated cells, and there is reason to believe that the core of the Pacinian body is also distinctly cellular in the earlier stages of its development. The core is surrounded, not by a single capsule only, but by a large number, twenty to sixty, of concentric capsules, which are crowded together towards the axis but wider apart in the more superficial regions. A longitudinal or transverse section of a Pacinian corpuscle accordingly exhibits a series of concentric lines separating spaces, the lines being especially close together near the axis. Each space represents a capsule or coat of connective tissue consisting of hardly more than fluid, traversed by transverse and longitudinal fibres, and defined by a membrane both on its inner and outer side. The lines in the section of a corpuscle represent the junctions of the inner membrane of one capsule with the outer membrane of the one lying to its inside. They are really the expression of lymphatic spaces, since each membrane of two adjoining capsules is covered with a layer of flat lymphatic epithelioid plates, the two layers leaving a linear space between them. Frequently a blood vessel entering into the corpuscle at the side is distributed to the capsules, or at least to the outer ones.

A single nerve-fibre approaches the base of the corpuscle and as it draws near undergoes a great development of its sheath of Henle, which becomes transformed into a series of concentric, or in section parallel, sheets of connective tissue separated by lymph spaces. After reaching the corpuscle the several sheets of the enlarged sheath of Henle leave the nerve-fibre in succession to become the capsules of the corpuscle; and when the nerve-fibre penetrates to the bottom of the core it consists only of axis, medulla, and neurilemma. The neurilemma is lost, passing off either to the innermost capsule or to the core itself; the medulla also disappears; but the axis cylinder is continued undivided up the axis of the core giving off on its way short lateral processes with knobbed endings. It ends in a blunt, somewhat swollen point, or more frequently dividing ends in a number of such terminal knobs. Sometimes the nerve-fibre passes straight through the corpuscle without ending; at the far end of the core it regains its medulla and neurilemma, takes up in turn the various capsules to form a thickened sheath of Henle, and leaves the corpuscle much as it entered it. In addition to the main nerve-fibre, many, and possibly all, Pacinian corpuscles receive a second fibre, which breaks up into a fine plexus of fibrils surrounding the main fibre.

It is obvious that in the Pacinian corpuscle as in the more minute end-bulb we have to do with a special development of connective tissue around an abruptly ending axis cylinder. The whole arrangement has the air of a mechanical device; but it would be hazardous to insist too much on this.

Pacinian corpuscles are found in abundance clustered round the nerve branches running in the subcutaneous tissue of the palmar surface of the hand and sole of the foot, especially in the regions of the digits. It has been calculated that about 600 are present in the under-surface of each hand, and about as many in each foot. They are much more sparse on, and often wholly absent from, the nerves of the skin in the back of the hand and foot, the upper arm and the neck. They occur on the nerves of the mamma and of the genital organs. They are very numerous along the nerves of the joints, especially in the flexures, about a hundred being counted at the elbow; they are also found along the periosteal nerves of the shafts of some bones, and occur occasionally in the inside of large nerve trunks. Lastly, they are scattered over the sympathetic nerves of the abdomen. It is obvious that their functional connection with cutaneous sensations is a very indirect one; but to this point we shall return.

§ **871.** *Grandry's corpuscles.* Although these are not found in connexion with the skin of man, or indeed with true skin anywhere, their occurrence being limited to the dermis of the mucous membrane of the beak, of the tongue, and of the palate of certain birds, it will be desirable to say a few words about them.

In its simplest, typical form a corpuscle of Grandry, about $50\,\mu$ in diameter, consists of two nearly hemispherical or dome-shaped cells placed with their flat surfaces face to face. Each cell contains a conspicuous round nucleus surrounded by granular cell substance; it has all the appearance of a large well-nourished epithelium cell. The two cells are surrounded by a capsule of connective tissue bearing nuclei. A medullated nerve-fibre with its neurilemma and sheath of Henle, approaching the corpuscle in a more or less coiled course, joins it at the side at the level of the junction of the two cells. Here the sheath of Henle, and probably also the neurilemma, becomes continuous with the capsule, the medulla ceases, and the naked axis cylinder passing in between the opposed flat surfaces of the cells ends in the centre between them in a round, flattened biconvex disc or "plate," forming as it were a "buffer" between the two cells in their central region. As far as can be ascertained there is no continuity between the axis cylinder plate and the substance of either of the cells; the former simply lies in contact with each of the latter. These epithelium cells, if we may venture so to call them, appear to be "subsidiary" cells, assisting in some unknown way the equally unknown functions of the terminal plate of the axis cylinder; and we may perhaps draw an analogy between them and the subsidiary cells of the organs of smell and taste. As we shall see, the nerves of the skin enter in the epidermis into similar relations with special cells distributed among the ordinary cells of the malpighian layer in certain situations.

Sometimes there are three such cells, the uppermost and undermost being hemispherical or dome-shaped, and the middle one having the form of a disc or short cylinder, all being surrounded by the same capsule. In such a case the nerve-fibre divides into two branches, one forming a terminal disc between the upper and middle cell, the other between the middle and lower cell. Where there are more than three cells the divisions of the nerve-fibre are correspondingly increased. Sometimes a compound corpuscle is formed by the aggregation of several simple corpuscles, each with its epithelium cells and one or more terminal plates of an axis cylinder.

§ **872.** *Touch corpuscles.* These are minute bodies of an oval form, 60 to $100\,\mu$ in the long diameter, which, in certain situations, are found in the papillæ of the dermis lying immediately beneath the epidermis. It is easy to recognize that each touch corpuscle contains a number of oval nuclei placed transversely, and that between the nuclei run irregular, but on the whole transverse lines, having the appearance of transverse fibres or septa, the whole being surrounded by an indistinct capsule. This arrangement gives the whole body an appearance not unlike that of a miniature fir cone. A medullated nerve-fibre, generally with a more or less coiled course, reaches the corpuscle, most commonly at the side, and after twisting round the body to a variable extent, and frequently dividing, is finally lost to view in the midst of the corpuscle. Sometimes the corpuscles appear compound, as if made up of more corpuscles than one joined together, the whole body appearing lobed.

It is easy to recognize this much; but the further details of the structure of a touch corpuscle are matters of great difficulty, about which much divergence of opinion obtains. Perhaps the view which at present most commends itself is to regard them as formed on the same plan as a compound corpuscle of Grandry, but with the constituent elements less distinct. According to this view the transverse nuclei are the nuclei of subsidiary cells, in connection with which the divisions of the axis cylinder of the nerve-fibre end in expansions comparable to the terminal plates of the corpuscle of Grandry, the characteristic transverse striæ being the expression of the divisions of the nerve-fibre. But in the touch corpuscle the subsidiary cells are not so well formed as in the corpuscle of Grandry, and moreover seem especially placed towards the surface of the corpuscle, leaving the interior free at least from nuclei; the division of the nerve-fibre is also more complete, the fibre often breaking up into clusters or bunches of branches; the medulla accompanies the dividing axis cylinder for a greater distance into the interior of the body; and the conspicuous terminal plates of the corpuscle of Grandry are replaced by mere slightly swollen knobs. Without insisting too much on the value of the analogy, we may probably conclude that in the touch corpuscle we have to do with an axis cylinder, which dividing frequently, ends abruptly in contact with, or in connection with, but not in continuity with certain cells of a peculiar nature.

Touch corpuscles are found in man most abundantly on the palmar surface of the hand, especially of the fingers. It has been calculated that the palmar surface of the tip of the forefinger contains about 100 touch corpuscles for each two square millimeters, that of the second joint 40, and that of the third joint 15 in a like area. They are also found, though somewhat less plentifully, on the sole of the foot and toes, about 30 being present in two square millimeters of the last joint of the great toe, and seven or eight in the like area of the middle of the sole. They occur in the nipple of the breast, on the under, volar, surface of the fore arm, being here however exceedingly scanty, at the edge of the eyelids and lips, and on the genital organs. They appear to be wholly absent from all parts of the body where hair is found.

§ **873**. We may now turn to the second kind of ending of nerve-fibres in the skin, that in which fibrils pass into the very epidermis. It will be useful to begin with the nerves of the cornea, the examination of which is relatively easy.

The medullated nerve-fibres, which enter into the body of the cornea at its circumference, soon lose their medulla and subsequently their neurilemma. The axis cylinders dividing form towards the front of the cornea a plexus called the 'primary plexus,' at the nodal points of which, as also occasionally on the bars of which, nuclei are seen. From this primary plexus bundles of fibrillæ form other plexuses in the substance of the cornea, especially in front, where beneath the anterior elastic lamina (§ 716) a plexus called the "sub-basal plexus" may sometimes be found. From this plexus, or directly from the primary plexus, bundles of fibrillæ, or divisions of axis cylinders, of some little thickness, run straight outwards to the epithelium, piercing the anterior elastic lamina, and hence called *rami perforantes.* Reaching the base of the lowermost, vertical tier of cells, each ramus breaks up into a pencil of delicate fibrils, which taking a direction at right angles to that of the ramus itself, and converging towards the centre of the cornea, form between the upper surface of the elastic lamina and the base of the lowermost tier of cells, a close-set horizontal plexus of delicate fibrils, the *subepithelial plexus.* From this subepithelial plexus still more delicate fibrils run upwards into the epithelium, forming between the cells an *intra-epithelial plexus*; and from this or directly from the subepithelial plexus, extremely fine fibrillæ pass upwards towards the surface of the epithelium. It has been asserted that these project beyond the surface, the free ends swollen into tiny knobs waving freely in the fluid which always covers the surface of the cornea. This however has been doubted; but in any case the nerves of the cornea send off branches which end in the manner described, quite close to the surface of the cornea as free fibrils, not directly connected with any cells. It need hardly be said that the detection of these fine endings requires special preparation; they are seen best with the gold chloride method.

§ **874**. A similar mode of ending also occurs in the skin. In all parts of the skin medullated nerve-fibres are present, assuming more or less a plexiform arrangement in the dermis close beneath the epidermis, the fibres being more numerous and their arrangement more intricate in some regions of the body than in others. These medullated fibres give off branches which, losing their medulla, penetrate into the epidermis, and there forming a more or less distinct plexus analogous to the subepithelial plexus of the cornea, give off numerous delicate fibrillæ which, forming a network among the cells of the malpighian layer, end in a manner similar to that obtaining in the cornea, namely, in free ends, between the cells of the upper region of the malpighian layer beneath the stratum granulosum; this latter layer apparently they never penetrate.

The penetrating fibres giving rise to these intraepithelial fibrillæ, pass into the epidermis at the tops and at the sides of the papillæ, as well as in the valleys between the papillæ. As far as can be ascertained, they are present in all regions of the skin, being probably more abundant in some regions than in others. Their relative abundance cannot be quantitatively determined with exactness owing to the inconstancy of the gold chloride method; in the same region the method will disclose at one time a very large number of fibrillæ, at another time very few. We are probably justified in asserting that this method of ending, by means of intraepithelial fibrillæ, is the general mode of ending of the afferent nerve-fibres distributed to the skin itself.

§ **875**. In the epidermis of the pig's snout there are found in the deeper regions of the malpighian layer between the papillæ and elsewhere, oval nucleated cells which differ from the ordinary cells of the layer, both in their form, being oval not polygonal, in the absence of prickles, and in their behaviour towards reagents, especially gold chloride, with which they stain somewhat deeply. Non-medullated nerve fibres penetrating the epidermis from the dermis, and dividing into branches, pass to these cells, which frequently occur in clusters, and each branch terminates in a sort of plate or disc, which is applied closely to the under surface of one of the cells, but apparently is not continuous with the substance of the cell. The cells are not so well developed as are the cells of a corpuscle of Grandry, and the terminal plate has not such a definite form as in that body; but the resemblance between the two is very striking. Moreover cells of this kind with the belonging nerve filaments have been observed lying partly within the epidermis and partly in the dermis beneath. It would seem as if these cells with their nerve filaments formed within the epidermis an organ of the same nature as and probably playing the same part as the corpuscle of Grandry in the dermis.

Similar cells, which have been called "touch-cells," have been observed in other regions of the skin of various animals, and are well developed in the outer root sheath or malpighian layer of the tactile hairs, such as those in the "whisker" of the cat. They have been found in man in regions where the touch corpuscles are sparse or absent, in the skin of the back, belly, arms, legs and neck. It seems probable that further investigation will disclose that they have a very wide distribution, and, as we shall see later, this mode of ending of the cutaneous nerves is probably of great importance.

## SEC. 2. THE GENERAL FEATURES OF CUTANEOUS SENSATIONS.

§ **876.** The sensations which we experience by means of the skin and cutaneous nerves appear, in the first instance, to be of at least three kinds. In the first place, all bodies, whatever their chemical or physical nature, be they gaseous, liquid or solid, when brought into contact with the skin, when made to exert mechanical pressure on the skin, produce sensations of a certain kind; these sensations, whose characters depend mainly on the amount of pressure exerted and on the region and area of the skin pressed upon, may be conveniently spoken of as *tactile sensations* or *sensations of touch proper.* In the second place, when either by actual contact with, or by the mere proximity of hot or cold bodies, of whatever nature, the temperature of an area of the skin is changed with sufficient rapidity, we experience sensations of a kind different from the tactile sensations just mentioned; these we may speak of as *sensations of temperature, sensations of heat and cold.* In the third place, when too violent a pressure is exerted on the skin, or when the changes of temperature are excessive, or when certain changes giving rise neither to tactile nor to temperature sensations are produced, or take place in the skin, we experience sensations which we call *sensations of pain.* This third kind of sensation stands, in many respects, apart from the other two, and it will be convenient to study sensations of pain by themselves. Sensations of touch proper and of heat and cold are much more akin and may be treated of together.

### *Tactile Sensations or Sensations of Pressure.*

§ **877.** Many of the characters of tactile sensations are of the same order as those of visual sensations, which we studied somewhat fully, and indeed similar characters may be more or less distinctly recognized in all sensations. The amount, that is to say the intensity of the sensation, varies with the amount of the stimulus, with the amount of pressure brought to bear on a given area of the skin; in giving rise to the sensation the pressure causes a deformation of the skin, and the amount of this deformation seems to determine the intensity of the sensation. Taking the same spot of skin, the tip of the forefinger, we can experimentally ascertain the minimum of pressure of which we can become conscious, such for example as that exerted by a minute fragment of some light body, pith or wool, falling through a certain small height. The minimum of pressure may also be satisfactorily ascertained by pressing on the skin with a fine object, such as a hair, the force necessary to make the hair bend having been previously determined. Starting from this minimum and increasing the pressure, we find the sensation also to increase up to a certain limit; and Weber's law (§ 747) holds good for tactile sensations, indeed may be more easily verified in their case than perhaps in the case of other sensations.

When two sensations follow each other in the same spot of skin at a sufficiently short interval they are fused into one; thus, if the finger be brought to bear lightly on the edge of a rotating card cut into a series of teeth, the teeth cease to be felt as such when they follow each other at a rapidity of about 1500 in a second. The vibrations of a cord cease to be appreciable by touch when they reach the same rapidity.

When two sensations are generated at the same time at two points of the skin too close together they become fused into one; but to this feature, which is of a different nature from the preceding, we shall return presently.

The sensation caused by pressure is at its maximum soon after its beginning, and thenceforward diminishes. The more suddenly the pressure is increased, the greater the sensation; and if the increase be sufficiently gradual, even very great pressure may be applied without giving rise to any sensation. Sudden relaxation of this pressure will, however, produce a very distinct sensation. And, indeed, both pressure and relaxation of pressure give rise to sensations, which, when of low intensity, may be mistaken for one another. A sensation in any spot is increased when the surrounding areas of skin are not subject to pressure at the same time. Thus if the finger be dipped into mercury the pressure of the mercury will be felt more at the surface of the fluid adjoining the skin which is not in contact with the mercury, than in the parts of the skin wholly covered with the mercury; and if the finger be drawn up and down, the sensation caused will be that of a ring moving along the finger. This effect may be compared with those of 'contrast' in visual sensations (§ 781).

All parts of the skin are not equally sensitive to pressure; the minimum of pressure which can be felt or the smallest difference of pressure which can be appreciated differs very much at different parts of the skin. Measured in this way, tactile sensations are much more acute on the palmar surface of the finger, or on the forehead, than on the arm or on the sole of the foot or on the back. In making these determinations all muscular movements should be avoided in order to eliminate the muscular sense of which we shall speak later on; and the area stimulated should be as small and the contact as uniform as possible.

In addition to the general differences of sensitiveness, it has been found that minute areas of the skin differ in their degree of sensitiveness to pressure. If a blunt pointed but otherwise fine needle be used to exert pressure, a little exploration will ascertain that at some points the amount of pressure can readily be recognized, while at other points, and these may be quite near the others, the amount of pressure cannot be recognized, and indeed no sensation is experienced until the pressure is excessive and then the sensation experienced is not one of touch proper but of pain. The points susceptible to pressure are known as "pressure" points or "touch" points. The points are most thickly distributed on the most hairy parts of the body, and appear, to some extent, to correspond with the hair follicles.

Small consecutive variations of pressure, as in counting a pulse, are more readily appreciated by certain parts of the skin, such as the tip of the finger, than by others. In all cases variations of pressure are more easily distinguished when they are successive than when they are simultaneous.

§ **878.** When anything touches a spot of our skin, we not only experience a 'pressure sensation' of greater or less intensity according to the amount of pressure exerted and the particular region of skin pressed upon, we are also at the same time aware that the sensation has been started in that spot, that the spot in question and not another has been touched. When we are touched on the finger or on the back we refer the sensations to the finger or to the back respectively, and when we are touched at two places on the same finger at the same time we refer the sensations to two parts of the finger. We localize our touch sensations with reference to the surface of our body after the same fashion that we localize our visual sensations with reference to the external world. Our whole skin serves us as a 'field of touch' analogous to the 'visual field' of the eye; and as when experiencing a visual sensation, we refer it to its presumed cause and say we perceive a light in some part or other of the field of sight, so when we experience a tactile sensation we say we perceive that something has touched this or that part of our skin; the tactile sensation has become a tactile perception. As the accuracy of our visual perceptions is largely dependent on the smallness of the retinal interval which must separate two simultaneous retinal stimulations in order that these shall give rise to two separate sensations, vision being most distinct in the fovea centralis where this interval is smallest, so also the accuracy of our tactile perceptions is dependent on the smallness of a like cutaneous interval. Where, as in the tip of the finger, the interval is small, contact with even a small area of surface may give rise to several simultaneous but distinct sensations, each of which we localize; and we thus obtain by means of one contact several perceptions affording a considerable amount of information concerning the nature of the surface. Where, as in the skin of the back, the interval is great, contact with even a large area of surface may give rise to one sensation, which we do not resolve into its components, all the several sensory impulses from the skin fusing into one common sensation; we only localize this one sensation, we have only one perception of something touching that part of our back, and the information which we thus acquire concerning the nature of the surface in contact with the skin is limited.

As the above remark indicates, the interval in question varies very widely in different parts of the surface of the body; our power of discrimination of separate stimuli is much finer in certain parts than in others. Moreover the distribution of the fineness of discrimination is not identical with that of the mere appreciation of pressure; some parts may be very sensitive and yet separate stimuli may be imperfectly distinguished. The magnitude of the interval of space which must separate two simultaneous stimulations of the skin in order that the two consequent sets of impulses may give rise to two distinct sensations may be conveniently determined for different regions of the skin by measuring the distance at which two points (preferably blunted) of a pair of compasses must be held apart, so that when the two points are in contact with the skin, the two consequent sensations can be localized with sufficient accuracy to be referred to two points of the body, and not confounded together as one.

The following tabular statement of results thus obtained may be taken as shewing in a general way the relative power of distinguishing two points in the more important regions of the surface of the skin.

| | |
|---|---|
| Tip of tongue ... ... ... ... | 1·1 mm. |
| Palm of terminal phalanx of finger ... | 2·2 „ |
| Palm of second „ „ ... | 4·4 „ |
| Tip of nose ... ... ... ... ... | 6·6 „ |
| White part of lips ... ... ... ... | 8·8 „ |
| Back of second phalanx of finger ... | 11·1 „ |
| Skin over malar bone ... ... ... | 15·4 „ |
| Back of hand ... ... ... ... | 29·8 „ |
| Forearm ... ... ... ... ... | 39·6 „ |
| Sternum ... ... ... ... ... | 44·0 „ |
| Back ... ... ... ... ... | 66·0 „ |

When fine points are employed, and these are placed on the "touch" points already described, the distances at which two points are discriminated on the different regions of the body are stated to be much smaller than in the above table, which is drawn up from observations made before the existence of such touch points was known.

As a general rule it may be said that the more mobile parts, or those which execute the widest movements, or execute movements most easily and frequently, such as the hands and lips, are those by which we can thus discriminate sensations most readily. The lighter the pressure used to give rise to the sensations, provided that the impulses generated are adequate to excite distinctly appreciable sensations, the more easily are two sensations distinguished; thus two compass points which, when touching the skin lightly, appear as two, may, when firmly pressed, give rise to one sensation only. The distinction between the sensations is obscured by neighbouring sensations arising at the same time. Thus two points readily distinguished as two when the skin is under ordinary conditions, are confused into one when brought to bear inside a ring of heavy metal pressing on the skin.

It need hardly be said that these tactile perceptions, like all other perceptions, are increased by exercise. We may speak of our 'field of touch,' as being composed of tactile areas or units, in the same way that we spoke (§ 754) of our field of vision as being composed of visual areas or units; but all that was there said concerning the subjective nature of the limits of visual areas, applies equally well, *mutatis mutandis*, to tactile areas. When two points of the compasses are felt as two distinct sensations, it is not necessary that two, and only two, nerve-fibres should be stimulated, or, putting the matter more generally, that two or only two discrete sets of sensory impulses, should travel along separate paths to separate cerebral centres. All that is necessary is that the two cerebral sensation-areas should not be too completely fused together. The improvement by exercise of the sense of touch must be explained not by an increased development of the terminal organs, not by a growth of new nerve-fibres in the skin, but by a more exact limitation of the sensational areas in the brain, as for example by the development of a resistance which limits the radiation taking place from the centres of the several areas.

### *Sensations of Heat and Cold.*

§ **879**. When we bring into contact with, or even into the immediate neighbourhood of a spot of skin, a body distinctly hotter than is the skin at the spot for the time being, we experience a special sensation; we feel something in the skin that was not there before, but that something is wholly unlike the effect of pressure, and we call the sensation a sensation of heat. The sensation is obviously due to the rise in the temperature of skin which is the direct effect of the contact with or the nearness of the hot body. Our skin has a certain temperature which varies from time to time, according to circumstances, and is not the same in all regions of the skin at the same time. A given spot of skin at a given time will have a certain temperature; that temperature does not give rise to a distinct sensation though its effects may enter into what we may call general sensibility; we may not be directly conscious, for instance, that the forehead has one temperature and the hand another, though the two temperatures may differ widely. It appears then that we are only conscious of a cutaneous sensation of heat when the temperature of a region of the skin which has previously been fairly constant is raised; we may add suddenly raised, for in sensations of heat as of pressure the stimulus must act with a certain rapidity in order to produce a distinct effect on consciousness.

If the body brought into contact with or near to the skin, instead of being distinctly hotter is distinctly colder than the skin we also experience a special sensation, a sensation of cold; and this sensation differs in kind not only from that of pressure, but also from that of heat. We might expect perhaps that since cold only differs from heat in degree, both being degrees of temperature, that the sensations of heat and cold would also be alike, differing only in degree; but when we appeal to our consciousness we recognize that they differ in kind. So long as sensations of heat and cold remain sensations of heat and cold, they appear to us not as merely different phases of the same thing but as quite unlike; when the exciting heat or cold is excessive we perhaps may fail to distinguish between the two, but that is because both are lost in the sensation of pain. It appears then that we are conscious of a specific sensation of cold when the temperature of a region of the skin which has previously been fairly constant is with sufficient rapidity lowered. To how large an extent we are, under ordinary circumstances, unconscious of the actual temperature of the skin and how sensitive we are to even slight changes of temperature may be illustrated by using one region of the skin as a stimulus of heat or cold for another. At a time, for instance, when we are not directly conscious of the hand being either colder or hotter than the forehead, by putting the one up to the other we may experience a distinct sensation telling us that the hand decidedly differs in temperature from the forehead; we feel at once that one is warmer or colder than the other, though it may take some little time to recognise which is the warmer or the colder.

§ **880**. These sensations of heat and cold behave very much in the same way as sensations of pressure. We have already said that the change of temperature like the change of pressure must be effected with a certain rapidity in order to produce a distinct sensation, and in general the more gradual the change the less intense is the sensation.

As might be expected from the fact that it takes a longer time to produce a change of temperature than to exert pressure, the sensation of either heat or cold is somewhat slowly developed and lasts some considerable time; hence consecutive sensations readily fuse into one.

Since it is the changed temperature and not the particular temperature arrived at which is the basis of the sensation, a hot body or a cold body gives rise to a sensation only at the first contact or approach and for some little time afterwards, the effect diminishing from the very moment that the change has been established. Hence a hot body or a cold body, even when kept itself at a constant temperature and not cooled or heated by contact with the cooler or warmer skin, ceases after a while to be felt as hot or cold. For this reason the repeated dipping of the hand into hot or cold water produces a greater sensation than when the hand is allowed to remain all the time in the water, though in the latter case the temperature of the skin is most affected.

The effects of contrast are obvious in sensations of heat and cold as in those of pressure; when the hand is dipped in hot water the sensation is most intense at the ring where the hand emerges from the surface of the water.

We can with some accuracy distinguish small differences of temperature, especially those lying near the normal temperature of the skin. In this respect these sensations follow Weber's law, though apparently slight differences of cold are more easily recognized than those of slight heat. The range of the greatest sensitiveness seems to lie between 27° and 33°.

The regions of the skin most sensitive to variations in temperature are not identical with those most sensitive to variations in pressure. Thus the cheeks, eyelids, temples and lips, are more sensitive than the hands. The least sensitive parts are the legs, and front and back of the trunk.

It has been found also that there are minute points which are especially sensitive to variations in temperature. If heat or cold be applied by means of a metal tube or rod narrowed to a point, it will be found that cold is readily appreciated at some points of the skin, and heat at other points. These minute areas are spoken of as 'heat' and 'cold' points respectively. The cold points are more definite than the heat points and their existence is more easily verified.

As with pressure sensations so also with sensations of heat and cold, two sensations excited at a certain distance apart may or may not be fused into one, the distance necessary for the separation of the sensations varying in different regions of the body, and being, as might be expected from the ease with which heat and cold are conducted, much greater than in the case of pressure sensations. We also 'localize' the sensations of heat and cold; we can recognize which region of the skin is being heated or cooled; and thus these sensations also enter into our perceptions of the external world.

**§ 881.** We have treated of the sensations of touch and of heat and cold as cutaneous sensations; but they are not confined to the skin commonly so called. We experience the same sensations in varying degree by help of the lining of the mouth and pharynx, which is called a mucous membrane; and they may also be traced for a short distance up the rectum beyond the margin of the skin proper. But in both these situations, the lining membrane is by origin and in structure epiblastic, that is to say cutaneous, and in possessing cutaneous functions shews its real nature. These functions are most marked at the beginning of the passages, the tip of the tongue being very sensitive to touch and heat and cold, with a well-developed power of localization; they are very rapidly lost in the rectum, and more gradually disappear at the lower part of the pharynx and in the œsophagus; a fluid which in the mouth is felt distinctly as hot gives rise to a sensation of pain not of heat when it is swallowed, and a cold or warm drink is only felt as cold or warm when swallowed in quantity sufficient to affect by conduction the abdominal skin. The maintenance of these cutaneous functions in the initial parts of the alimentary canal, which are under the dominion of the will, is, like the sense of taste, a safeguard against the introduction into the canal of noxious substances; in the subsequent parts, no longer subject to the will, any warning which such sensations might give would be too late and useless.

## SEC. 3. ON PAINFUL AND SOME OTHER KINDS OF SENSATION.

§ **882**. When excessive pressure is exerted on the skin, or when the change of temperature passes certain limits, the sensation which is excited ceases to be recognized as one either of touch or of temperature and takes on characters of its own; we then call it a sensation of pain. In this respect the skin as a sensory organ appears at first sight to differ from the other organs of sense which we have studied. We have no evidence that simple stimulation of the retina, however excessive, will give rise to pain, meaning by pain the kind of sensation we feel when the skin is cut or burnt. We often speak it is true, especially in cases of disease of the eye, of exposure to light causing pain, but the pain in such cases is felt through the eyeball, not through the retina and optic nerve; the pain is not an excessive development of visual sensations, it is a phase of that sensibility which the subsidiary structures of the eye share, in common as we shall see presently, with not only the skin but nearly all other structures of the body. In like manner we have no evidence that an auditory or an olfactory or a gustatory sensation can, through mere intensity, become converted into a sensation of pain, though we may, in the act of hearing, smelling or tasting, receive sensations of pain from the ear, nose, or mouth. We often of course apply the word 'painful' to a sound, or a group of visual sensations, or a smell, or a taste; but that is in the sense of being exceedingly disagreeable, and has reference to our classification of the complex psychical effects of all our sensations into those which are pleasurable and those which are painful. Without entering into any psychological analysis, we may assume that the pain which we feel when the finger is cut is a wholly different thing from the pain which is given to a most delicately musical ear by even the most horrible discord; and in what follows we shall use the word pain in the first of these two meanings.

§ **883**. The above considerations suggest that in the case of the skin as in the cases of the other organs of special sense, a sensation of pain is not simply an exaggeration of a sensation of pressure or of a sensation of temperature, but is a separate sensation, developed in a different way in the skin, a sensation which may override and so seem to replace the sensation of pressure or temperature developed at the same time, but which must not be confounded with it. And this view derives support from the fact that events taking place in many other parts of the body, from which we experience sensations neither of touch nor of temperature, may under favourable circumstances give rise to pain in varying degree. When, for instance, a tendon is laid bare contact with a body will not produce tactile sensations, heating or cooling will not produce temperature sensations; one cannot by means of the tendon as one can by means of the skin perceive that a rough or smooth body, that a hot or cold body, has been brought to act upon it. Indeed in respect to all structures other than the skin and nerves, to such structures, namely, as muscles, tendons, ligaments, bones, and the viscera generally, there is a large amount of experimental and clinical evidence shewing that, so long as these are in a normal condition, experimental stimulation of them does not give rise to any distinct change of consciousness; a muscle or a tendon, the intestine, the liver, or the heart may be handled, pinched, cut, or cauterized without any pain or indeed any sensation at all being felt or any signs given of consciousness being affected. Nevertheless when the parts are in an abnormal condition even slight stimulation may produce a very marked effect on consciousness. If, for instance, a tendon becomes inflamed, any movement causing a change in the tendon, especially one putting the tendon on the stretch, will affect consciousness and give rise to a sensation. But the sensation is one of pain and not of any other kind. Moreover we simply 'feel' the pain, we do not 'perceive' the cause of it; because we feel the pain we infer that something has caused it, but we cannot from the nature of the pain itself decide whether that something is a stretching of the tendon, the contact of a hard or soft body, the approach of some hot or cold body, the application of some chemical substance, the passage of an electric current, or intrinsic events taking place in the tendon itself as the result of physiological changes. And so in other instances; there is hardly a part of the body changes in which may not, under certain circumstances, give rise to sensations of pain. We can to a variable extent, in a more or less ill-defined manner, localize the sensation; we can distinguish a pain in the foot from one in the leg, a pain in the thumb from one in a finger; we may occasionally fix the pain in a very small limited area, though especially if the sensation be intense, the pain radiates and its localization becomes obscure. And we may here remark that when we thus localize a pain arising in the structures of which we are speaking, we refer the pain not to the structures themselves but to neighbouring parts and especially to the skin; the intense pain, for instance, of "renal colic," caused by the impact of a calculus in the ureter is referred by us not to the ureter itself but to adjoining parts, to the corresponding somatic segment; and so in other instances. We can also recognize certain characters in different pains, beyond that of the mere degree of intensity; we speak of pains as being burning, aching, gnawing, cutting, throbbing, and the like. But in all cases the pain remains a mere sensation; when it comes, all we can say is that we feel in a particular region of the body a pain of a certain intensity and having a certain character. We infer that something is wrong, but the pain in no way tells us what the wrong is; we may call the pain a burning one because it is more or less like the pain which we feel when the skin is burnt; but in the vast majority of cases heat has nothing whatever to do with pains of a burning character; and so with other kinds of pain, the character of the pain does not in itself tell us anything about its cause.

Are we then to regard pain as a sensation of a kind by itself, the very threshold of which, the very least amount of which that can in any way affect our consciousness, must be regarded as already pain? In attempting to answer this question the following considerations deserve attention.

We are in a certain obscure way aware of what we may call the general condition of our body. To put an extreme case, if the whole of our abdominal viscera were removed we should be aware of the loss. We should be aware of this through more ways than one. The tactile sensations from the abdominal skin would be in such a case different from the normal, and moreover the muscular sense of the abdominal walls and of all the muscles whose actions bear on the abdomen, would make us aware of the void. But beyond all these indirect ways, it is probable that we should in a more or less obscure manner be directly conscious of the loss. It is probable that sensory impulses, not of the character of pain, are continually, or from time to time, passing upwards from the abdominal viscera to the central nervous system. These do not affect our consciousness in such a distinct manner as to enable us to examine them psychologically in the same way that we are able to examine special sensations such as those of sight, or even sensations of pain; they are even less well defined than those of the muscular sense; nevertheless they do enter, though obscurely, into our consciousness, so that we become aware of any great change in them, and they have been spoken of under the title of "common" or "general sensibility." In discussing (§ 643) the manner in which the manifold coordinate movements of the body were carried out we saw reasons for thinking that the central processes of the nervous system were largely determined by varied afferent impulses which produced their effects without giving rise to any sharp and decided change of consciousness; many of these are probably afferent impulses of the common sensibility of which we are now speaking.

If we suppose that the skin in common with the other tissues of the body possesses this common sensibility, and if we further suppose that in the skin as elsewhere, these afferent impulses when developed, as is the case under normal circumstances, to a slight extent only are not distinctly recognized by consciousness, and that when they do assume such a magnitude or intensity as to break in upon consciousness the change of consciousness which they produce is of the kind which we call pain, we reach a conclusion which is also supported by other considerations. On the one hand such a view is in accord with the conclusion that cutaneous sensations of pain are wholly distinct from and developed in a wholly different way from sensations of touch and temperature; and, as we shall see, to this conclusion we are led by several different arguments. On the other hand it relieves us from the following difficulty. It may happen to a man to suffer pain in a particular region or tissue of the body, once only in the course of his lifetime, or possibly not even once; nay, we may suppose that in this or that region or tissue pain is felt once only in one individual among a large number of persons. If we suppose that pain is not as suggested above an excessive phase of something which is continually going on in a lower phase, but a something by itself quite distinct from all other sensations, we are driven to conclude, since such a sensation must have a special mechanism, including special afferent nerve-fibres to carry it out, that in the case in question such a mechanism of pain has been preserved intact but unused through whole generations in order that it may once in a while come into use; which is in the highest degree improbable. This difficulty disappears if we suppose that the constantly smouldering embers of common sensibility may be at any moment fanned into the flame of pain.

We may conclude then that the skin in common with other tissues possesses common sensibility, and that when this is excited in excess, so as to distinctly affect consciousness, we call it pain. We thus experience through the skin three kinds of sensations, those of touch, of temperature, and of common sensibility, but the two former only are developed by further psychical processes into perceptions; it is by them alone that we obtain through the skin knowledge of external objects.

§ **884.** There is another consideration to be taken into view. The agents which applied to the skin produce pain, act violently on the skin, in many cases injuring the epidermis and affecting the dermis. Moreover if the epidermis be removed, and the stimulus, mechanical, thermal, or chemical, be applied to the dermis or to the nerves running in it, we still experience sensations of pain, though no longer those of touch and temperature; when a sharp or hot body is made to touch, not the intact skin but a wound, we suffer pain, but do not recognize the sharpness or the heat which is causing the pain.

It has been suggested that painful sensations, like those of touch and temperature, are brought about by means of special terminal organs, and certain facts have been brought forward in favour of this view. It has been stated, on the one hand, that stimulation of certain parts of the body, as the cornea and conjunctiva, only produces pain. There is no doubt, however, that this is not correct; by suitable stimulation of both cornea and conjunctiva sensations of touch may be produced wholly free from any element of pain. On the other hand there is a strip of the mucous membrane of the cheek which appears to be insensitive to pain; stimuli which are distinctly painful elsewhere, produce here only sensations of touch.

It has also been stated that there are certain minute areas in the skin which are especially sensitive to pain. Similar areas have been described in the cornea, conjunctiva and mucous membranes, and these have been regarded as "pain" points analogous to touch and temperature points. There is, however, much reason to believe that these sensitive points are spots at which nerve fibrils or nerve endings come near the surface of the skin and such observations do not necessarily point to the existence of special endings for pain sensations. We may conclude that the evidence for the existence of such endings is much less definite than in the case of touch and temperature.

§ **885**. *Hunger and thirst.* We may introduce here the few words that we have to say concerning two affections of consciousness, which may perhaps be considered as kinds of sensation, namely, hunger and thirst.

We refer our feelings of thirst to, or at least we associate them with, a particular condition of the mucous membrane of the mouth, especially of the soft palate. When the mucous membrane of this region becomes drier than normal, as for instance by being exposed to too great an evaporation, we feel 'thirsty,' and the feeling is at once removed by adequately moistening the membrane. Under ordinary circumstances however the condition of thirst is brought about, not by anything bearing specially or exclusively on the mucous membrane of the soft palate or even of the whole mouth, but by the diminution of the water present in the body either through restriction of the intake, or through excess of the output in the secretions, such as that of sweat, or through both together. This is often spoken of as diminution of the water of the blood; but most probably the specific gravity of the blood is kept constant by the withdrawal of water from the lymph, so that the loss falls on the latter fluid. Such a diminution of the water of the body may be brought about by circumstances such as excessive sweating which in themselves do not cause special dryness of the mucous membrane of the soft palate; this part then undergoes a loss of water in common with the other tissues, but not in a special degree. Nevertheless thirst thus brought about may be temporarily assuaged by simple moistening of the soft palate. From this we may infer that the sensation of thirst is brought about by afferent sensory impulses started in the mucous membrane of the soft palate by a deficiency of water in that membrane, perhaps by a drain on the lymph spaces of that membrane.

We are in the habit of assuaging thirst by drinking water, or watery fluids, and in doing so produce both a direct local effect on the palate and a general indirect effect on the body. In the absence of the local effect, the indirect effect is slow in coming and needs a large quantity of fluid; when in cases of gastric fistula water is introduced into the stomach through the fistulous opening, large quantities may be given before thirst is assuaged.

The sensation of hunger is in a somewhat similar manner referred to, or associated with, the condition of the gastric mucous membrane. We feel hungry when the stomach is empty. But even more distinctly than in the case of thirst the main cause of the sensation seems to be a general condition of the body, namely, that produced by the products of digestion ceasing to be thrown into the blood. The sensation is not due to the mere emptiness of the stomach, though the emptiness of the stomach is one of the results of the abstinence from food; for the feeling of hunger may disappear though the stomach may remain empty, if adequate nourishment be conveyed in other ways, as by injection into the bowels; conversely even we ourselves may under abnormal conditions feel hungry on a full stomach, and in some animals, herbivora, the stomach is always more or less full. The sensation however does seem to be in some way specially connected with the condition of the gastric walls, much in the same way that thirst is specially connected with the palate; the products of digestion have a much greater power in appeasing hunger when they act locally and directly on the gastric membrane than when they are simply brought to bear on the body at large, and a small quantity of food will immediately satisfy hunger when introduced into the stomach, though it will have no effect when introduced otherwise. Moreover our own consciousness clearly connects the sensation in some way or other with the stomach.

As to what is the particular change in the gastric membrane which thus gives rise or assists in giving rise to the sensation we know little or nothing; indigestible substances such as cannot be properly called food when taken into the stomach at least temporarily remove the sensation. And we have little or no knowledge as to the particular nerves which serve as the paths for the afferent impulses which we may suppose to be generated in the gastric membrane. Division of the vagus nerve on both sides is said to have no effect on hunger; from this we may conclude that the impulses do not pass up this nerve, though it appears to be the sensory nerve of the stomach. But we have no evidence that the impulses pass along the sympathetic nerves.

Allied somewhat to hunger is the peculiar feeling which we may perhaps also speak of as a sensation, known as nausea, the precursor of vomiting (see § 272) and brought about like vomiting by a variety of events. We have little or no knowledge of it viewed as a sensation.

The affection of consciousness which is produced by the form of cutaneous stimulation known as "tickling" is of a peculiar character, differing from tactile sensations. Indeed it is probably undesirable to speak of it or of other psychical effects of cutaneous stimulation as a sensation, since it seems to be not the direct effect of the sensory cutaneous impulses, which are probably ordinary tactile impulses, but rather the effect on consciousness of changes in the central nervous system brought about by those sensory impulses.

## SEC. 4. ON THE MODE OF DEVELOPMENT OF CUTANEOUS SENSATIONS.

§ **886.** Our studies so far point to the conclusion that sensations of touch and temperature stand on the same footing as visual, auditory, and other special sensations; and it will be profitable now to compare in some detail the former with the latter. In doing so we may, in order to make the matter more simple, confine ourselves in the first instance to sensations of touch proper, that is to sensations of mere contact and pressure, discussing later on the relations of these to sensations of heat and cold.

In studying vision we came to the conclusion that the undulations of the ether so affect the rods and cones and other retinal structures as to give rise to visual impulses, and that these visual impulses, travelling up the fibres of the optic nerve to the visual centres, gave rise by means of those centres to the affections of consciousness which we call visual sensations; we may leave aside in the present instance all reference to the complexity of the visual centres.

We obtained absolute proof that the only way in which light can give rise to visual impulses in the optic fibres is by acting on the retinal structures. Since the optic fibres are the only nerve-fibres in direct connection with the retinal structures visual impulses can be carried by them alone. As we pointed out we know absolutely nothing about the nature of visual impulses themselves; our conclusions concerning the various characters and kinds of visual impulses are simply deductions from the psychological examination of our sensations; our objective knowledge of them is limited to the fact that when light falls on a functionally active retina an electric change is developed in the optic fibres. As we mentioned in § 750 the statement that stimulation of the optic fibres themselves, as when the optic nerve is cut with a knife, gives rise to visual sensations, has led to the adoption of the view that any impulse passing along the optic fibres, however started, whether by the action of light on the retina, or by direct stimulation of the fibres themselves, gives rise to a visual sensation and must therefore be regarded as a visual impulse.

This view, under the title of the doctrine of " the specific energy of nerves," has been extended to the nerves of the other special senses and indeed to nerves in general. This doctrine teaches that, owing either to the constitution of the central ending of a sensory fibre or to that combined with the nature of the fibre itself (the view may also be adapted to motor fibres), whatever impulses are generated in the fibre can give rise to those events only which are specific to that central ending, impulses of all kinds along an optic fibre giving rise to visual sensations, impulses of all kinds along an auditory fibre giving rise to auditory sensations, and so on. Hence under this view the purpose of the specific terminal organ is simply to allow the specific stimulus of the sense, light in the case of the retina, to develop impulses in the specific nerve, a result which, in the absence of the terminal organ, it is powerless to achieve.

We saw however (§ 750) that according to some observers direct stimulation of the optic fibres, as when the nerve is cut, does not produce visual sensations, and therefore does not give rise to visual impulses; so far as can be ascertained such a stimulation of the fibres appears to produce no effect at all on the central nervous system. It is clear that the specific energy in question cannot have its seat in the nerve-fibre, and additional evidence of this in the case of motor nerves is given by the fact, that when the central end of the cut vagus is united with the peripheral end of the cervical sympathetic, regeneration will take place, and after this has occurred stimulation of the vagus will cause opening of the eye, dilation of the pupil, constriction of the vessels of the ear, and other effects ordinarily produced by stimulating the cervical sympathetic. We must therefore modify the doctrine of the specific energy of nerves in the following way. We must suppose that; in the case of the optic nerve for instance, the visual centres are so constituted that they are stirred up to the development of visual sensations by the advent only of those kind of impulses which are started by means of the terminal organ. Since electric changes are developed in the optic fibres as in other nerve-fibres when the optic fibres are directly stimulated, we may infer that direct stimulation does lead to nervous impulses; and we may further infer that these reach the visual centres but are unable to develop visual sensations because they are not true visual impulses such as are generated by help of the terminal organs.

This modified view is supported, though the support is of a negative kind only, by the behaviour of the other organs of special sense. We have no satisfactory experimental or other evidence that stimulation of the auditory fibres or of the olfactory fibres otherwise than through the terminal organs will give rise to auditory or olfactory sensations. We have evidence that stimulation of the centres by various means will give rise to the specific sensations, but not that stimulation of the fibres of the nerves themselves will. The branches of the glossopharyngeal and fifth nerves distributed to the organs of taste are, unlike the above, mixed nerves, and when they are stimulated sensations other than specific taste sensations are also developed, and the former might obscure the latter; still the evidence so far as it goes supports the view that stimulation of gustatory fibres otherwise than through their terminal organs does not lead to the development of gustatory sensations.

In the case of touch the evidence is perhaps still stronger. We must in any case suppose that each cutaneous nerve distributed to a given area of skin contains fibres which subserve the sense of touch exercised by that area, and which pass from the terminal organs in that area, whatever their nature, to the parts of the central nervous system, whatever they may be (§ 679), which act as centres of touch sensations. If these fibres when directly stimulated, apart from their terminal organs, necessarily give rise to touch sensations, stimulation of the nerve itself while running in the subcutaneous tissue should give rise to touch sensations. But experience shews, as we said a little while ago, that this is not the case. Whenever the nerve-fibres themselves are directly stimulated, as for instance when the epidermis is removed from the skin or when a nerve is laid bare, then however they be stimulated, be the stimulus weak or strong, if consciousness be affected at all, the affection takes on the form of pain; psychological examination of the subjective result discloses nothing that can be called a sensation of touch. A familiar instance of the difference between the effects of stimulating a nerve trunk, and those of stimulating the cutaneous terminal organs of special sense, is seen in the effect of dipping the elbow into a freezing mixture. The cold affects the skin of the elbow and gives rise to sensations of cold in that part; but the cold, if intense enough, also affects the underlying trunk of the ulnar nerve, and by direct stimulation of the fibres in the trunk develops sensory impulses; these impulses however are those not of sensations of cold, but of pain; and the pain, in accordance with a principle to which we shall presently call attention, is referred to the terminal distribution of the ulnar nerve on the ulnar side of the hand and arm. In speaking above (§ 883) of pain we said that excessive pressure or excessive heat or excessive cold applied to the skin, overrides or annuls pressure and temperature sensations and gives rise to mere sensations of pain; and it might be urged that when a nerve is directly stimulated the specific sensations of touch and temperature are similarly annulled. But in the case of the skin an excessive or violent stimulation is necessary to produce this effect, whereas a nerve may be directly stimulated by so slight a stimulus as to give rise to hardly more than discomfort without distinct pressure or temperature sensations being felt; and we can hardly suppose that in such a case these are present but are annulled by an amount of pain so slight as that which is produced. Thus making every allowance for the suggestion that sensations of pain may override and obscure concomitant sensations of touch and temperature, we seem driven to the conclusion that the latter sensations can only be developed by help of special terminal organs, and that a stimulation of the nerve-fibres themselves if it produces any effect at all on consciousness gives rise to pain, and to pain alone.

We are in this way led to conceive of the skin as provided on the one hand with specific fibres ending in specific terminal organs and serving for sensations of touch and temperature, and on the other hand with fibres of common sensibility having no such specific terminal organs, the two kinds of fibres being mixed together in the common cutaneous nerve. These fibres moreover have not only different peripheral but also different central endings, and during at least some part of their course run in different tracts or in a different manner in the central nervous system; for as we saw in treating of the central nervous system (§ 683) cases of disease of the central nervous system have been recorded in which over certain cutaneous areas sensations of touch had been lost, while common sensibility and sensations of pain remained, or *vice versâ*. We may add that the difference between the central paths or endings of the nerves of touch and those of pain is further shewn by the fact that in certain nervous diseases (tabes) when the skin is pricked with a pin, the contact of the pin may be felt as mere touch for so long a time as one or two seconds before pain is felt; the diseased condition enormously delays the transmission of the impulses of pain but has not so much effect on those of touch.

§ **887**. We may go a step further; there is a certain amount of evidence that the terminal organs and fibres concerned in touch proper, in sensations of pressure, are different and separate from those concerned in sensations of heat and cold. In the first place the general topographical distribution over the surface of the body of sensitiveness to pressure is different from that of sensitiveness to temperature. A familiar instance of this is seen in bringing the palm of the hand to touch the forehead. In the former the sense of touch is highly developed, in the latter the sense of temperature; hence with the forehead we feel that the hand is warm or cold, with the hand we feel that the forehead is rough or smooth; at least these two feelings respectively preponderate, the one in the one part, the other in the other. In the second place, cases of disease of the central nervous system of the spinal cord have been recorded in which, over certain cutaneous areas, sensations of pressure were lost but sensations of temperature remained, and *vice versâ*. In the third place, if the stimulation of the skin be confined to extremely minute areas, if the pressure or the change of temperature be brought to bear as much as possible on a mere point of the skin, it has already been pointed out (§§ 877 and 880) that some points of the skin are sensitive to pressure but not to change of temperature, while others again are sensitive to change of temperature but not to pressure. Further, the points of the skin which are sensitive to pressure are those which are not sensitive to heat or cold, and *vice versâ.* Such results as these are only intelligible on the supposition that the terminal organs for pressure are different from those for heat and cold and differently distributed over the surface of the skin.

§ **888.** The punctiform method of exploring the sensitiveness of the skin has further led to a result which is unexpected and indeed presents difficulties. Heat and cold in themselves differ only in degree; they are positive and negative phases of the same thing. We should therefore naturally expect that the same terminal organs would be employed for sensations both of heat and of cold, and that the same points of the skin would be alike sensitive both to heat and to cold. But as we have already seen (§ 880), points which are sensitive to heat are insensitive to cold and *vice versâ.* Indeed it is stated that a cold point will develop a cold sensation even when stimulated by heat, and this "paradoxical" sensation, as it has been called, points very strongly to the existence of separate terminal organs for the two qualities of temperature Moreover this result is in accord with results gained otherwise. If the arm or leg be "sent to sleep" by pressure on the brachial or sciatic nerves the skin will be found at a certain stage to be little sensitive to cold though distinctly sensitive to warmth. So also the whole surface of the glans penis, in contrast to the prepuce, is very slightly sensitive to cold, but distinctly sensitive to warmth. On the other hand, the conjunctiva and cornea are distinctly sensitive to cold, while, in most individuals at any rate, they appear to be wholly insensitive to heat. Moreover cases of disease of the central nervous system have been recorded in which the skin of a limb was sensitive to warmth, that is to degrees of temperature above that of the limb, but insensitive to cold. It may be remarked that in these cases, as in that of the limb "gone to sleep," the sensations of touch proper and of cold seem to run together and sensations of pain and of heat also to run together.

It seems probable then from these considerations that we possess three sets of terminal organs and three sets of fibres, one for pressure, a second for heat and a third for cold. It must be borne in mind however that the three sensations are not wholly independent, since sensations of pressure are modified if changes in temperature be taking place at the same time in the same spot of skin. Thus a penny cooled down nearly to zero and placed on the forehead will be judged by most people to be as heavy or even heavier than two pennies of the temperature of the forehead itself, that is to say, the sensation of pressure is increased by a concomitant sensation of cold; and a similar modification of the sensation of pressure is also often observed when the object pressing is not colder but warmer than the skin pressed on. A similar effect seems to be shewn in certain cases of disease of the central nervous system in which it has been recorded that a hot body such as a heated spoon was felt when brought in contact with the skin, though the same spoon applied at the temperature of the skin itself produced no sensation at all, and the heated spoon was recognized not as a hot body, but simply as something touching the skin. The exact explanation of these facts is not very clear, but it may perhaps be argued that the effect is brought about amid the central processes through which the sensations are developed and does not shew that the sensations have common terminal organs.

§ **889**. In attempting to understand the nature of the peripheral events through which the sensory impulses giving rise to sensations of pressure of heat and of cold are developed two or three matters must be borne in mind. In the first place, as we have already said, though the skin has a temperature of its own, we are not directly conscious of that, or at all events are not distinctly conscious of it in the same way that we become conscious of any sudden change in that temperature; nor indeed are we, except in extreme cases, distinctly conscious that the temperature of one region differs from that of another, or that the temperature of the same region gradually varies from time to time. It would seem as if the development of a clear and distinct sensation was largely dependent on the contrast as to temperature between an area of the skin and surrounding areas; and indeed we have already pointed out the marked effects of contrast. The same applies to pressure; we are not, at least distinctly and directly, conscious of the uniform pressure of the atmosphere over the whole surface of the body, when we stand naked in still air. We are not however justified in assuming that under the above circumstances nothing whatever is taking place in the sensory nerves of the skin, that when we feel a sensation the change in the sensory apparatus (using that phrase in its widest sense to include both peripheral and central parts) is one from absolute quiescence to activity; it is not impossible, and some facts indeed seem to suggest, that even when we feel no distinct cutaneous sensations, afferent impulses still continue to stream onwards from the periphery to the central nervous system, supplying as it were a groundwork of nervous events which enter largely in various ways into the conduct of the whole body, but which do not distinctly affect consciousness. If this be so, we may infer that the affection of consciousness which we call a sensation is the immediate effect of an adequately large change in this groundwork, rather than of a set of quite new isolated impulses passing straight up from the peripheral organ to the "seat of consciousness."

In the second place, when we do experience sensations of temperature the sensation is caused not by the mere change of temperature but by the altered condition of the skin which results from that change. When an area of the skin having a normal temperature is brought in contact with a cold body, the skin undergoes a change from a normal to a lower temperature, and we experience a sensation of cold. Now, if it were only the change from a normal to a lower temperature which gave rise to the sensation, though the sensation might and probably would last much longer than the change itself, it could not be prolonged by the mere maintenance of the lower temperature when once the change had been established. But experience shews that it is; we still feel a sensation of cold, at a time when the contact of the cold body is not producing any further lowering of temperature and at most is only maintaining the lower temperature already brought about. Nay, more, the sensation of cold continues after the cooling body has been removed, at the time when the skin is returning to its normal temperature, that is to say, is undergoing the very opposite change of temperature, namely, one from cold to heat. And the same considerations apply to sensations of heat.

§ **890**. We may conclude then that when the application of cold or of heat to the skin causes a sensation of cold, the cold or heat produces a condition in the material of the skin, which condition starts nervous impulses in the afferent nerves of cold and heat sensations. Since the application of cold or of heat to the nerve-fibres underlying the skin does not produce a sensation of cold or heat, but only a sensation of pain, we may further conclude that the material whose condition starts the sensation is placed in the skin itself, in the epidermis or in the immediately underlying dermis. Since we experience sensations of cold and heat in regions of the skin, not only free from touch corpuscles but also free from any dermic terminal organs as yet known, the "points" of the skin determined experimentally to be points of cold and heat sensations, having been repeatedly found when extirpated to be free from all such dermic organs, we may, though with less certainty, still further infer that the material exists somewhere in the epidermis. We may add that sensations of temperature may be felt in the cornea, from which all dermic terminal organs seem certainly to be absent. And our knowledge that the nerve-fibres end as fine fibrillæ between and among the cells of the malpighian layer (§ 874) brings us to the final conclusion that the material of which we are speaking is to be sought for either in the fine nerve fibrillæ themselves, or, as seems more likely, in some or other of the cells of the malpighian layer specially connected with those fibrillæ.

Beyond this we cannot go; and even admitting thus much, it is difficult to understand how, if the change be one from a higher to a lower temperature, the lower temperature, whatever may have been the exact degree of the higher temperature, should in giving rise to sensations of cold affect one set of fibres only, or how the higher temperature should similarly affect another set of fibres only; but we must leave the matter here.

The considerations which have just been brought forward in relation to sensations of heat and cold, may be also applied to sensations of pressure; with regard to them also we are driven to the conclusion that they take origin in the lower layer of the epidermis through some condition brought about by the pressure. We can appreciate pressure by the cornea, from which as we have said dermic organs are absent. If the 'points of skin' in various parts of the body, determined experimentally to be points of pressure sensation, be extirpated and examined it is found that dermic organs are not necessarily present; indeed such points of pressure sensations do not differ essentially in structure from points of heat or cold sensations, though some slight difference in the manner of distribution of the dermic nerve filaments has been described.

We have, however, some reason to believe that there is a relation between 'touch' points and hair follicles, and it has been suggested that the terminal organs of touch on those parts of the body covered with hair are contained in the hair follicles, possibly in the outer root sheath as in the case of 'tactile' hairs (§ 875). Touch corpuscles, on the other hand, are found especially in those parts of the skin where hair is absent and it seems likely that these bodies may be the terminal organs of touch for the hairless regions of the skin while some structures in the hair follicles are the terminal organs for those parts where hair is present. This view would account for the remarkable prominence of touch corpuscles in those parts of the skin in which touch is most sensitive, while their absence in other parts would be accounted for by the existence of other organs to replace them. The evidence on these points, however, is not yet conclusive and the evidence as to the functions of the end-bulbs and of the Pacinian bodies is still less definite.

## SEC. 5. THE MUSCULAR SENSE.

**§ 891.** Before we go on to deal with some of the psychical aspects of cutaneous sensations it will be desirable to speak of certain sensations accompanying and belonging to the movements of the body which are carried out by means of the skeletal muscles. These sensations, which are in many ways related to or mixed up with cutaneous sensations, are often spoken of as constituting a "muscular sense," but this term must not be taken to imply that the muscles are the only, or indeed the chief, source of these sensations.

When we examine our own consciousness we find that we are aware of the position of the several parts of our body. In this we are under ordinary circumstances assisted by sight; but sight is not necessary. If for instance, with the eyes shut, we place the arm in any attitude, we are aware of the attitude and can describe, or by movements of the other arm imitate with considerable accuracy the details of the attitude, the relative positions of the upper arm, forearm, hand, fingers and the like. If we change the attitude by moving the arm or part of the arm we can, though the eyes be still shut, tell the amount and characters of the change.

Again, when we examine our own consciousness we find that we possess a measure of the amount of resistance to our movements which we from time to time meet with. When we come into contact with an external object we are conscious not only of the pressure exerted by the object on our skin, but also of the pressure which we exert on the object; we can appreciate the amount of effort which we make to produce by pressure an effect upon the object. A similar appreciation of our own efforts assists us largely in forming a judgment as to the weight of an object. If we place the hand and arm flat on a table, we can estimate the pressure exerted by a body resting on the palm of the hand, and so come to a conclusion as to its weight; in this case we are conscious only of the pressure exerted by the body on our skin. If however we hold the body in the hand, we not only feel the pressure of the body, but we are also aware of the exertion required to support and lift it. And we find by experience that when we trust to this appreciation of the amount of effort needed to lift an object as well as to sensations of pressure, we can form much more accurate judgments concerning the weight of the object than when we rely on sensations of pressure alone. When we want to tell how heavy a thing is, we are not in the habit of allowing it simply to press on the hand laid flat on a table or otherwise at rest, we hold it in our hand and lift it up and down.

The above instances deal with three things which it might be desirable to keep separate, namely, 'position,' 'movement' and 'effort'; it might seem desirable to speak of "a sense of position," "a sense of movement," and "a sense of effort." But, if we leave out of consideration the problems connected with our appreciation of the position of the head, which as we have seen seems especially dependent on afferent impulses passing up the auditory (vestibular) nerve, we may say that the position of the various parts of our body is so closely dependent on movement, that is on the contraction of skeletal muscles, some muscle or other playing its part in almost every position and every change of position, that in the discussion on which we are now entering it will be hardly profitable to distinguish between the two; and we may use the term "muscular sense" to denote our appreciation both of movement and of position resulting from movement.

§ **892**. There are more valid reasons for distinguishing between our appreciation of an effort and our appreciation of the movement which is the result of that effort. For the view has been put forward and supported by argument that when we make a muscular effort, we are directly conscious of the nervous processes of the central nervous system underlying the effort, that the changes in the central nervous system involved in initiating and executing a movement of the body so affect our consciousness that we have a sense of the nervous effort itself, of the innervation as it has been called; and it is urged that the condition of the central nervous system through which we appreciate the nature and magnitude of the effort is thus the direct effect of central changes, and not the outcome of afferent impulses proceeding from the part moved.

Whether it be the case or not that consciousness is thus directly affected by changes in the central nervous system, such for instance as those taking place in the motor cortical area or in the pyramidal tract, the evidence goes to shew that any such affection has, at most, very little share in that appreciation of our movements which is generally called "the muscular sense." Not only is our appreciation of passive movements very similar to our appreciation of active movements (we are as well aware of an attitude in which our arm has been placed by others as of one in which we have placed it ourselves), but also if a muscular contraction be brought about not by any action at all of the central nervous system, but by the direct electric or other stimulation of the muscles or motor nerves, the muscular sense of the movement which results differs little from that of a like voluntary movement. If for instance, while our eyes are shut the wrist be bent by direct stimulation of the flexor muscles, we are aware of the movement and can appreciate its character and amount; we can even use such an artificial movement to judge of weight and resistance. It is indeed urged that our judgment under such conditions is less secure than when the movement is a voluntary one; and from this it is argued that our judgment is at least assisted by our appreciation of the central changes by a "sense of the effort" as distinguished from a muscular sense of peripheral origin; but even this is disputed. We may at least conclude that our appreciation of our movements and muscular efforts is largely, if not wholly, dependent on what may be called a muscular sense which is the outcome of afferent impulses proceeding from the periphery and started in the parts concerned in the movement.

§ **893**. Coming next to the questions, What is the exact nature of these afferent impulses? In what tissues are they started, and along what paths do they travel? we find the answers beset with considerable difficulties. Every movement of the body, even a simple one, is in reality a complex affair, and the carrying it out involves changes in several tissues. In the first place there are changes in one or more muscles, changes of contraction in active movements, of extension and relaxation in passive movements. In the second place there are changes in the skin which during a movement is in one spot stretched, in another relaxed or folded; and in movements of locomotion the pressure of the foot on the ground is continually changing. In the third place, by far the majority of movements affect a joint, and hence involve changes in the relations of the articular surfaces, in the capsule and ligaments and in the tendons. All these are possible sources of afferent impulses.

Now we know that the skin is a source of afferent impulses and so of sensations, namely, the sensations of pressure, of temperature and of pain; and we may fairly suppose that stretching or slackening the skin gives rise to impulses either analogous to those caused by the pressure of an external object or, it may be, of a nature more akin to those which belong to general sensibility. Hence it is possible that these do at least contribute, under normal circumstances, to what as a whole we call the muscular sense.

Indeed it is maintained by some that these cutaneous impulses furnish the whole basis of what is called the muscular sense, the name on this view being of course erroneous. In attempting to judge of such a view we may appeal on the one hand to our own consciousness, and on the other hand to the phenomena of incoordinate movements. In a previous part of this work, § 643, we dwelt upon the importance of afferent impulses as factors in the coordination of movements. We have had occasion repeatedly to insist that all the movements of the body, a large number of those which are involuntary as well as all those which are voluntary, are guided by afferent impulses, and that in the absence of these afferent impulses the movements are apt to become uncertain and imperfect, or even to fail altogether. We need not here repeat what we have previously urged; it is sufficient for our present purpose to say that conspicuous among these afferent impulses are those which form the groundwork of the muscular sense; at times they may do their work without directly affecting consciousness but at other times they bring about a distinct affection of consciousness, and it is this affection of consciousness which is more properly called the muscular sense.

Now, on the one hand, we find upon examination that coordination of movements is not distinctly affected by the diminution of cutaneous sensations, but may be maintained in the absence of cutaneous sensations and indeed in the absence of the skin. Thus frogs are said to be able to execute their ordinary movements without signs of incoordination after the whole skin has been removed. Cases of nervous diseases have been recorded in which, if not complete absence of, at least great failure in, cutaneous sensations has not been accompanied by any loss of coordination. And if we appeal to our own consciousness we do not find the muscular sense notably diminished by temporary anæsthesia of the skin; if, for instance, the skin of the arm be rendered for a while anæsthetic, we do not find any marked change in our power of judging weights or resistance, or in appreciating, with the eyes shut, the position of the limb.

On the other hand we find recorded cases of nervous diseases in which loss of coordination, and loss of the muscular sense, as indicated by the difficulty or inability to judge weights and resistance and to recognise with the eyes shut the position of the limbs or other parts of the body, have occurred without notable loss of cutaneous sensations. This is often strikingly shewn in cases of the disease or group of diseases known as "tabes dorsalis," often spoken of from one of its prominent symptoms as, "locomotor ataxy," the conspicuous pathological condition of which is a structural change in the posterior columns of the lower part of the cord. In certain stages of this disease the patient may retain good cutaneous sensations, he may experience tactile, temperature and painful sensations in the skin of his legs, for instance, and possess adequate muscular strength in his legs, and yet, from want of coordination, be unable to move them properly unless he be assisted by sight. So long as his eyes are open he may be able to stand and walk, but if his eyes are shut he often falls, and when he moves, moves with a staggering uncertain gait; he fears, in the dark, to go up or down stairs even though he knows them well.

When a direct appeal is made to his consciousness he appears to possess little or no muscular sense; he is unaware, so long as his eyes are shut, of the position of the limbs affected by the disease, and if the arms are affected is unable properly to judge weights.

These cases of "tabes" are very varied in their symptoms, which indeed alter as the disease advances. Concerning them and similar phenomena presented by other allied nervous diseases there has been much discussion; but the evidence afforded by them, supported as it is to a certain extent by experimental results, is strongly in favour of the view that the afferent impulses which determine coordination and which go to make up what we are now calling the muscular sense are other than those started in the skin.

We may therefore dismiss cutaneous sensations as not being essential factors of the sense.

§ **894**. There remain on the one hand the muscles, on the other the joints with the ligaments and tendons around them; the afferent impulses under discussion must come from one or other or both of these.

Against the view that the afferent impulses of the muscular sense come from the muscles themselves has been urged the fact that, tested experimentally, muscular fibres in a normal condition possess a very feeble general sensibility; when a muscle is cut or pinched comparatively little or, according to some observers, no pain is felt; it is only under abnormal circumstances, as when a muscle is inflamed, that direct stimulation of this kind causes pain; and the pain which we feel in cramp is similarly the product of an abnormal condition, for even an extremely violent muscular effort does not cause us actual pain.

This argument however is not valid, for not only may it equally well be applied to the other set of tissues, tendons, ligaments, and the like, which in a normal condition possess a similarly feeble general sensibility, but it supposes that the muscular sense is merely a development of general sensibility, not a special sense like that of touch. We have no positive reasons for this supposition, and arguments based on the analogy of the skin oppose it. We have seen reason to regard the cutaneous sensations of pressure and temperature as wholly distinct from those of general sensibility, that is to say of pain; and we may conclude that the muscular sense is similarly a special sense, similarly distinct from affections of common sensibility in either muscular fibres or their connective tissue appendages.

On the other hand afferent impulses may proceed from muscles, for when a nerve twig going to a muscle is stimulated centripetally, after division, reflex movements result; if the stimulus is weak the movement is confined to the muscle itself (we are supposing that other nerve twigs going to the muscle are left intact); if the stimulus is strong, the movement spreads to neighbouring muscles. And we know that a muscle is supplied by nerve fibres which do not end in end-plates in the muscular fibres; some of these are vaso-motor, but others are afferent, and have been found to end in definite structures within the muscle which have been called "muscle spindles." These structures have a rough resemblance to Pacinian corpuscles. A muscle spindle has a capsule consisting of concentric lamellæ but these are less numerous and less regular in arrangement than those of a Pacinian corpuscle. Within the capsule is a lymph space and the centre or core is composed of a bundle of striated muscle fibres surrounded by a sheath of connective tissue. The spindle is richly supplied with medullated nerve fibres which experiment shews to be derived from the cells of the ganglion of the posterior root of the spinal cord.

Tendons and ligaments are also provided with afferent nerve fibres, and a special mode of ending, a plexiform arrangement of fibrils terminating in minute end-bulbs, has been described in tendons under the name of the "organ of Golgi." The joint surfaces are also supplied with sensory endings, rounded end-bulbs being found in these situations.

Both muscles on the one hand, and tendons, ligament and joint surfaces on the other, are then provided with structures which are capable of acting as the terminal organs of the afferent impulses of which we have been speaking. We must seek therefore other arguments to decide whether the muscular sense is derived from the muscles or from other parts. We cannot by an appeal to our own consciousness localize the sensation so as to lodge it either in one tissue or another, and must trust to indirect indications. On the one hand there seems to be a close connection between the muscular sense and the 'sense of fatigue'; and the latter appears to be determined by the condition of the muscles. Again, in many of our movements we only employ a part of a muscle, and it is difficult to suppose that the afferent impulses which guide us in using that part only, depend only on the effect which the partial use of the muscle produces in the tendons and the like. On the other hand, when we have a muscular sense of the movements of the fingers, we can hardly suppose that the sense is afforded by impulses coming exclusively from the muscles moving the fingers, distant as these often are from the joints which they move. And, again, the movements of which we are most distinctly sensible, are especially the movements affecting joints; indeed we have some difficulty in appreciating the amount and character of a movement not necessarily involving a joint such as one caused by contractions of the orbicular muscle of the mouth or of the eye, even though in these cases we are assisted by cutaneous sensations.

There are other facts which are strongly in favour of the view that the joint surfaces, tendons or other structures in the neighbourhood of joints are the chief sources of the afferent impulses.

By passing a strong faradaic current for some time through a limb, it is possible to greatly diminish the sensitiveness of the intervening structures. When a current has been passed in this manner through the muscles of the arm, it is found that movements of the elbow may be estimated as accurately, or even more accurately, than in the normal condition. If, however the current be passed through the elbow joint, the power of estimating movement is found to be very seriously affected. The surfaces of the joints would seem to be of the most importance and, indeed, it is easy to understand how the gliding of joint surfaces over one another, with the varying relations of the two surfaces, would give rise to a series of sensations which might very well act as the basis of our perception of movement.

We ought therefore to conclude that the muscular sense though probably based in part on impulses derived from the muscular fibres is mainly based on impulses derived from the joints, tendons and other passive instruments of the muscles, though we cannot as yet assign accurately the relative share. If this be so the 'muscular' sense is not a wholly appropriate term; but it would be undesirable, at present at least, to attempt to replace it by a new one.

This muscular sense, using the term in its broad meaning, enters largely into our life. By it we are not only enabled to coordinate and execute adequately the various movements which we make, but through it we derive much of our knowledge of the external world. Through it we are also conscious of the varying condition of the several parts of our body even when the muscles are at rest; the tired and especially the paralysed limb is said to 'feel heavy.' In this way the state of our muscles and other tissues largely determines our general feeling of health and vigour, of weariness, ill health and feebleness.

The fact that the Pacinian bodies are found around joints has led to the suggestion that these serve as the terminal organs of the muscular sense. The appearance of these bodies suggests that they are capable of responding to the variations of pressure which would be produced by movements of the joints. It is probable however that several kinds of terminal organ in different situations are stimulated by the movement of a limb and that all of them, the Pacinian bodies included, contribute to the sum of changes upon which our perception of movement and position is based.

## SEC. 6. ON TACTILE PERCEPTIONS AND JUDGMENTS.

§ **895.** As a means of gaining knowledge of external things the sense of touch ranks next in importance to that of sight. Auditory sensations enter largely and in several ways into our life; they serve as an important means of communication; together with smell and taste they afford pleasure and guide our acts; but, as regards our direct knowledge of the external world, we learn by means of them very little compared with what we learn by sight and touch. To a certain extent we make use of touch by itself; we bring the surface of a body into contact with some region of the skin such as the finger, and by the several sensations which we receive either from several points of that region at the same time, or from one or more points in succession, we learn certain characters of the surface, whether for instance it is rough or smooth. We thus also ascertain whether the body be hot or cold; and we may, within certain limits, form a judgment of the size of the surface by simply estimating the size of the area of our skin with which the body can be in contact at the same time.

But though we may and do thus base conclusions on tactile perceptions alone, we most frequently employ touch in association with sight on the one hand and with the muscular sense on the other.

The ties indeed between touch and the muscular sense are many and close. When we explore the nature of a body by touch we press the skin, of the finger for instance, on the body; and we do that not merely in order to determine to what extent the tactile sensation is increased by the increase of pressure, but also and indeed chiefly to ascertain the amount of resistance to pressure which is offered by the body. But that resistance, through which chiefly we judge whether the body be soft or hard, is appreciated not by the tactile but by the muscular sense.

Or again, placing the finger on the surface of a body, and moving the finger over the surface in such a way that the contact, as judged by the pure tactile sensation, remains the same, we find that in one case the movement has been continued in the same plane, whereupon we judge the surface to be flat, that in another case the finger has been gradually carried out of the plane, whereupon we judge the surface to be curved, and that in the third case the movement of the finger has been irregular, whereupon we judge that the surface is irregular; and so on. In each case we estimate the movement by the muscular sense, and thus by a combination of muscular sense and of touch we form a judgment of the conformation of external bodies. In the same way, and indeed as part of the same process, by a combination of the muscular sense and of touch we estimate the size of external objects. By a like double act we estimate the position in space in relation to our body of such objects as are within our reach, such as can be touched either directly by one of our limbs or indirectly by help of a stick or otherwise. So closely bound together are the muscular sense and the sense of touch proper, that in common language we speak of learning this or that by touch, when we really employ both senses.

§ **896**. No less close are the ties between sight and touch; indeed a very large part of our psychical life is built up on the association of visual and tactile sensations. There is no part of the external world, including our own bodies, which we can explore by touch, which we cannot, either directly or by optical aids such as mirrors, also explore by vision; and our conceptions of the nature of all such things is the outcome of a combination of the two senses, or rather bearing in mind what has just been said, of the three senses, sight, touch and the muscular sense. It is relatively easy to recognize blindfold, by touch alone, the characters of objects with which we are already previously familiar by help of vision; but it is very difficult to form by touch alone an accurate judgment of the form and size of objects which we have never seen. Were we limited to sight alone, we should form one set of conceptions of the world, were we limited to touch we should form another; and the two sets would be different.

In the conceptions which we form in actual life the two are combined. The congenitally blind are limited to one set only; and, when, as has happened in cases of congenital cataract, those who have been blind from birth are restored to vision after they have grown up and have accumulated a store of tactile conceptions, they fail at first to connect their new visual sensations with their old tactile experience. The stories of the first experiences in vision of such persons, as that for instance of the man who had to feel a cat in order to connect the visual image with his previous tactile image, and having carefully felt it all over said "Now, Puss! I shall know you again," illustrate the close dependence on each other of visual and tactile normal perceptions. This is also indicated by the zeal with which in former days the question was discussed whether a man who had been born blind and restored to sight in adult life, could recognize at first sight and by sight alone a cube, a square, and a sphere. It is perhaps especially in relation to size and space, that the two senses work together.

There are no converse cases of persons who, born without touch, and trusting to sight alone have, in later life, had touch restored to them; but there are many things within our vision, which are beyond our touch at the moment and some which we can never touch at any time; our conceptions of these latter are more or less uncertain, and the direct visual sensations have to be strengthened or corrected not by mere sensations but by intellectual efforts and reasoning. A group of visual sensations, constituting a visual image, may have an ordinary objective cause, but may be an ocular illusion; and the test which we at once apply to determine this is that of touch; the ordinary idea of a 'ghost' is that of a something which we can see but cannot touch, which excites visual sensations but affords no tactile sensations. Conversely a touch by something invisible, a touch as of a body which we ought to be able to see but cannot, we also recognize as unreal. The concordance of touch and vision affords in fact to a large extent the standard by which we judge of the reality of things.

§ **897.** The last remark naturally leads to the statement that as in the case of the other sensations, so in the case of the several cutaneous sensations, we may have sensations which are not due to their ordinary objective causes.

We have seen that visual sensations may arise from changes in the retina started not by light but by other agents, mechanical and others; and the question presents itself, Can touch proper, the sensation of pressure, be excited otherwise than by pressure and sensations of temperature by changes in the skin other than those of temperature? No very definite answer can be given to this question, though the case quoted above (§ 888) in which a heated spoon applied to the skin produced a sensation not of heat but of contact, points perhaps to the affirmative, as does also the fact that electric currents applied to the skin may produce sensations, pricking sensations, which if not identical with, may at least be confused with those of pressure.

Cutaneous sensations of all kinds may however be of central origin, may be due to changes in the central nervous system quite independent of all events in the skin, and may yet be referred to this or that region of the skin and to the objective cause which ordinarily gives rise to the sensation. Painful sensations indeed may rise from changes not only in the central organs but at any part of the whole length of the nerve, all being referred to the cutaneous terminations of the nerves on which the cause of pain is usually brought to bear. Tactile and temperature sensations as we have said cannot originate in changes in the nerves themselves, but they may arise through changes in the central organs; we may be subject to tactile phantoms comparable to ocular phantoms. Compared with visual sensations however our tactile sensations are so to speak fragmentary. A momentary exposure of the retina may fill the mind with a complex visual image, full of the most varied incident; but the tactile impressions which we can receive at any one moment are few and simple. Hence our tactile phantoms are also simple; we may fancy that some invisible garment has swept past us, or that a scorching flame has passed near us, we may feel that the hand or that the head is swollen and large, and we may experience an imaginary pain in every region of the skin in turn; but the most that we can thus feel is simple compared with the possible complexity of an ocular or even an auditory phantom.

§ **898.** Like other sensations our tactile sensations while they sometimes give us trustworthy information of the external world at other times may give rise to illusions. This is well illustrated by the so-called experiment of Aristotle. It is impossible in an ordinary position of the fingers to bring the radial side of the middle finger and the ulnar side of the ring finger to bear at the same time on a small object such as a marble. Hence when with the eyes shut we cross one finger over the other, and place a marble between them so that it touches the radial side of the one and the ulnar side of the other, we recognize that the object is such as could not under ordinary conditions be touched at the same time by these two portions of our skin, and therefore judge that we are touching not one but two marbles. The converse experiment will also succeed. If the outer sides of the crossed fingers are touched simultaneously by two objects, we seem to have one object between the fingers. Here two portions of the skin are touched by two objects which in the normal position are always touched by one object, and we have consequently the idea of one object. Upon repetition however we are able to correct our judgment and these illusions tend to disappear.

# INDEX.

Aberration, *see* Spherical, Chromatic
Accommodation, facts of, 1265–1272; near and far limits of, 1266, 1268; under water, 1270; for near objects, how effected, 1270; lost by removal of lens, 1272; mechanism of, 1283–1287; nervous mechanism of, 1295–1297; imperfections in, 1298; for two different colours, 1418
Acid tastes, 1516, 1517, 1519
Acoustic apparatus, for transference of auditory vibrations, 1435
Adaptation of retina, in dark, 1323; colourless spectrum of dark-adapted eye, 1360, 1370
Afferent nerves of skin, 1522; their part in muscular sense, 1554–1556; of tendons and ligaments, 1557
After-image, of visual sensations, 1326; negative, 1349; described, 1380, *et seq.*; positive and negative, 1381, 1382
After-tastes, 1516
Air cells of mastoid bone, 1438
Albinos, the absence of pigment-epithelium in, 1368
Albuminous glands of membrane of mouth, 1509, 1511
Alimentary canal, tactile sensations in, 1536
Alkaline tastes, 1514
Amacrine cells, 1314
Ambos, *see* Incus
Amphibia, mechanism of accommodation in, 1286; constriction of pupil in, 1295
Ampulla, position and structure of, 1454; function of, 1494
Anabolic phase, in metabolism, 1346, 1382
Annulus tympanicus, 1439
Antrum mastoideum, 1438
Anvil bone, *see* Incus
Aqueous humour, localities of, 1258; refractive powers, 1260, 1261; nutritive supply of, 1420, 1421; description of, 1422–1424; resembles cerebro-spinal fluid, 1422
Aristotle's experiment, 1562
Arteria centralis retinæ, *see* Central artery of the retina
Arteries, *see under* Central, Ciliary, &c.
Assimilation, 1348
Associated movements of pupils, 1296
Astigmatism, 1299
Atmospheric pressure, temporary deafness due to increase or decrease of, 1451
Atropin, action of, on pupil, 1291, 1295, 1296
Auditory epithelium, structure of, 1430, 1431, 1462; molecular movements in, 1493
Auditory field, compared with the visual, 1497
Auditory hairs, 1462; of crustacea, 1488
Auditory impulses, production of, 1434; paths of, 1435, 1446, 1458; length of, compared with length of sensation, 1483; development of, 1487–1495; synthesis of, 1493
Auditory judgments, 1496–1500
Auditory nerve, its functions in the coordination of movement, 1430, 1553; connection with otic vesicle, 1431; composition of, 1453; connection with labyrinth, 1455; with canalis cochlearis, 1459; path of, 1459
Auditory ossicles, position of, 1434, 1438; functions and action of, 1435, 1487; attachments of, 1439; regarded as a lever, 1443; 'damping' functions of, 1446
Auditory passage, external, effect of filling with fluid, 1497
Auditory perception, 1496–1500
Auditory phantoms, 1496
Auditory sensations, development of,

1430, 1434; on the nature of various, 1477-1486; distinction of, 1480; length of, compared with length of stimulus, 1483; recurrent, 1497
Auditory teeth, 1465
Auricle, *see* Pinna
Axis, *see* Optic axis
Axon, of cone-cell, 1313; of bipolar cells, 1314; of ganglionic cell, 1315

Bacterium photometricum, 1367
Basal cells, structure of, 1463; of olfactory mucous membrane, 1502
Basal membrane, *see* Membrane of Bruch
Base line of the eyes, 1389
Basilar membrane, position of, 1465; structure of, 1466; measurements of, 1476, 1492; number of fibres, 1476; theory of action of auditory impulses on, 1491
Beats, in sound, 1484
Binasal olfactory sensations, 1506
Binaural hearing, 1498
Binocular vision, 1388-1408; nature of mechanism of, 1414
Bipolar cells of the inner nuclear layer, 1313
Birds, mechanism of accommodation in, 1286; cones of eye in, 1374; cochlea of, 1456, 1476, 1495; Herbst corpuscles in, 1523; Grandry's corpuscles in, 1525
Bitter tastes, 1514, 1517
Black, the sensation of, 1336; colours mixed with, 1340; nature of the sensation according to Hering's theory, 1349
Blind spot, 1362; filling up the vacancy caused by, in field of vision, 1410
Blindness, pressure, 1371
Blinking, mechanism of, 1426; use of, 1428
Blood vessels, of choroid proper, 1274; of iris, effect of dilation of, 1288; of retina, 1318, 1319; retinal, rendered visible, 1365; of the eye, 1419; conjunctival, 1419; *see* Arteries, Veins, &c.
Blue, wave-lengths of, 1342; as a primary colour, 1351; wave-length of unchanging, 1352; in colour-blindness, 1357 *et seq.*; by evening light, 1360, 1370
Blue blindness, 1358
Bony labyrinth, position of, 1433, 1436; structure, 1455
Bowman, *see* Glands of, *and* Membrane of
Brain, retina considered as a piece of the, 1308; of visual sensations in, 1372; action of visual impulses on, 1377
Bright colours, defined, 1341, 1350; variations in spectrum, 1359, 1360
Browns, production of, 1340
Bruch, *see* Membrane of
Buccal membrane, effect of acids on, 1516
Bulb of eye, no change in form of, in accommodation, 1270
Buzzing in the ears, 1496

Calcium carbonate, in endolymph, 1464
Camera, the eye considered as a, 1258
Canal of Petit, 1282
Canal of Schlemm, 1280, 1419, 1423, 1424
Canaliculi, *see* Lachrymal
Canalis cochlearis, position of, 1453, 1456; structure of, in different mammals, 1475; length, in man, 1476
Canalis reuniens, 1454, 1476
Capillaries of choroid, 1274, 1419; of retina, 1319; rendered visible, 1366
Capsule of the lens, 1281; imperfections in, 1303; blood vessels of, 1420
Cardinal points, of optical system, 1259, 1261; of reduced eye, 1262
Carotid artery, internal, position of, 1288
Cartilage, tarsal, *see* Tarsus
Catheterism of Eustachian tube, 1451
Cavernous sympathetic plexus, position of, 1288
Cells of auditory epithelium, 1462; of the cornea, 1277; of the lens, 1280, 1281; of Corti, 1472; of Deiters, 1472; of membrane of Reissner, 1466; of taste-buds, 1510; *see also under* Bipolar, Ganglion, Goblet, &c., &c.
Central artery of the retina, early development of, 1254, 1257; position of, 1318, 1419
Central canal, 1424
Central process, *see* Axon
Central vein, of retina, position of, 1318, 1319
Centre of rotation of eyeballs, 1388
Centrifugal optic fibres, 1316, 1321
Cerebro-spinal fluid, resemblance to aqueous humour, 1422
Cervical sympathetic nerve, position of, 1288, 1289; effect on the pupil of division of, 1292; stimulation of, causes tears, 1428; effect of stimulation of, on eyelids, 1427
Cephalopods, mechanism of accommodation in, 1286
Chambers of eye, anterior and posterior, development of, 1258, 1276; fluid of, 1423
Chemical constitution and physiological action, 1505, 1514
Cholesterin in the lens, 1281
Chorda tympani, connection with the gustatory apparatus, 1520
Choriocapillaris, 1419
Chorio-capillary membrane, 1274, 1419

Choroid, early development of, 1256; structure of, 1257, 1273; pigment of, 1275; iridescence of surface, 1275; movement of, in accommodation, 1284; connection with optic nerve, 1306; blood vessels of, 1419; lymph-spaces, 1421
Choroid plexus, resemblance to ciliary processes, 1422
Choroidal fissure, formation of, 1254
Chromatic aberration, 1301
Ciliary arteries, of choroid, 1274, 1419; veins, of choroid, 1274
Ciliary ganglion, 1288
Ciliary muscle, position of, 1257; structure of, 1279, 1280; action of, in accommodation, 1284, 1286; longitudinal, 1280; circular, 1280
Ciliary nerves, action of, in accommodation, 1285; position of the short and long, 1288
Ciliary processes, of eye, 1256; structure of, 1275; pigment of, 1275; blood vessels of, 1419; resemblance to choroid plexus, 1422; fluid furnished by, 1423
Ciliary zone, structure of, 1278
Circumvallate papillæ, *see* Papillæ
Cisterna of labyrinth, 1455
Claudius cells, 1468
Coats of eye, *see* Choroid, Sclerotic, &c.
Cocaine, effect of, on gustatory organs, 1519
Cochlea, position of, 1433; base of, 1438; position and structure of, 1456; structure of, 1464–1476; in various animals, 1476; some data concerning the cochlea of man, 1476; functions of, 1494; absent in fishes, 1495
Cochlear nerve, direction of, 1459; connections and structure of, 1473–1475
Cold, *see* Sensation of heat and
Cold points, 1535, 1548
Colour-blindness, 1352–1361; explanation of the causes of, by the Helmholtz and the Young theories, 1354 *et seq.* in a single eye, 1356; total, 1358, 1370
Colour equations, defined, 1338; in varying illuminations, 1370
Colour sensations, 1336–1361; fusion of, 1337, 1418; complex character of, 1339; characters of a colour, 1340; production of non-saturated colours, 1343; curves of primary sensations, 1344; the four unchangeable colours, 1352; variations in, 1352; variations according to intensity of stimulus, 1358; simultaneous and successive contrast in, 1382; *see also* Primary sensations
'Colour top,' experiments with, 1338
Columnar epithelium cells of organ of Corti, 1468
Combination tones, 1485
Complementary colours, defined, 1341; a list of, 1342
Common sensibility, 1539
Cone bipolar cells, *see* Bipolar
Cone fibre, 1312
Cones, *see under* Rods and
Cones of Macula lutea, 1317; measurement of, 1333
Conjunctiva, structure of, 1278; blood vessels of, 1419; lymphatic vessels of, 1421; structure of, 1427; sensitive to cold, 1548
Connective tissue, of sclerotic coat, 1273; of choroid coat, 1273
Contrast, *see* Simultaneous, Successive
Coordination of visual sensations, 1376; of movements of eye, 1402; nervous mechanism of, 1405; of movement of body, function of vestibular nerve in connection with, 1494
Cornea, development of, 1256; structure of, 1258, 1260, 1277; surfaces of, 1260; radius of curvature of, 1261, 1262; measurement from anterior surface of, to anterior surface of lens, 1261; no change in curvature, for accommodation of eye, 1270; tears on the, 1302; blood vessels of, 1419; lymph-spaces, 1421; nerves of, 1527; sensitive to cold, 1548
Corneous layer, of membrane of mouth, 1508
Corpus quadrigeminum, connection with ocular movements, 1406
Corpuscles, of sclerotic, 1273; of cornea, 1278
Corresponding points, 1391
Corti, *see* Cell of, Organ of, Rods of
Cover cells, *see* Subsidiary cells
Cranial nerves, their action in coordination of ocular movements, 1402, 1405
Crista acustica, position and structure of, 1456, 1460; function of, 1488
Crocodile, cochlea of, 1495
Crustacea, auditory hairs of, 1488
Cup of organ of Corti, 1476; *see also* Retinal cup
Cupula of auditory hairs, 1462, 1489
Cutaneous sensations, 1522, *et seq.*; general features of, 1529; mode of development of, 1544–1551; and muscular sense, 1555, 1559
Cylinder cells, of auditory epithelium, 1463; of olfactory epithelium, 1501

Dalton, his colour-blindness, 1353
'Damping' organs of auditory apparatus, 1489
Dark, adaptation of retina in, 1323
Dark-adapted eye, colourless spectrum of, 1360, 1370
Dark colours defined, 1341
Deafness, temporary, caused by increase

or decrease of atmospheric pressure, 1451
Decussation, optic, effect on the pupils, 1291
Deep colours defined, 1341
Deiters, *see* Cell of
Delirium tremens, hallucinations of, 1387
Dendrite, of bipolar cells, 1313, 1314; of ganglionic cells, 1315
Dermis of conjunctiva, 1427
Descemet, *see* Membrane of
Desmours, *see* Membrane of
Diagrammatic eye, *see* Schematic
Dichromic vision, of the colour-blind, 1353; the colours of, 1357
Difference tones, 1485
Diffusion circles defined, 1265
Dilatator iridis, 1276
Dilator muscle, theory of existence of a special, 1295
Dioptric apparatus, imperfections in, 1298–1305
Dioptric mechanisms, defined, 1253; of the eye at rest, 1258–1264
Diplopia, crossed and uncrossed, 1393
Disparate points, defined, 1393
Dissimilation, 1348
Distance, visual perception of, 1413, 1415
Distinct vision, region of, 1331, 1332
Donders, his attempted amalgamation of the Young-Helmholtz and the Hering theories, 1372
Double vision, 1403
Duck, Herbst corpuscles in, 1523
Ductus endolymphaticus, 1454
Dural sheath of optic nerve, 1306

Ear, general structure of, 1430–1451; internal, 1433; exhaustion of, 1482; use of the form of external, 1499
Eel, constriction of pupil in, 1295
Effort, sense of, 1553
Elbow, effect of dipping in a freezing mixture, 1546
Electrical phenomena, their close connection with optical, 1366
Electrical stimulation of retina, 1328, 1386; of tongue, 1513, 1514, 1519
Ellipsoidal body, position of, 1310
Emmetropic eye, limits of accommodation for, 1268, 1269; considered as the normal eye, 1298
End-bulbs, localities for, and structure of, 1522, 1523; functions of, 1551
Endolymph, in otic vesicle, 1431; composition of, 1464
Entoptic phenomena, 1302; rule for direction of movement of, 1305
Entotic phenomena, 1496
Epidermic cells, nerve-endings in, 1522
Epidermis of pig's snout, 1528
Epithelium of the lens, 1280; of nasal mucous membranes, 1501–1503; of mucous membrane of mouth, 1508; treatment with gold chloride, 1527, 1528; *see also under* Auditory, &c.
Epitympanic cavity, position of, 1459; region, 1438
Eserin, *see* Physostigmin
Ether, vibrations of, 1366
Eustachian tube, position of, 1434, 1437; structure and functions of, 1450
External canal, *see under* Semicircular
External ear, *see* Ear
Extractives, in aqueous humour, 1422
Eye, general structure of, 1253–1258; early development of, 1254; diagram of relations of various parts, 1255; a camera, 1258; schematic, of Listing, 1261, 1262; the 'reduced' eye, 1262; nerves of, 1288; fluorescence of media of, 1305; colour-blindness in one eye, 1356; colourless spectrum of dark-adapted eye, 1360, 1370; co-ordination of the movements of, 1402; nutrition of, 1419–1425; blood vessels, 1419; lymphatics, 1420; protective mechanisms of, 1426–1429; opening and shutting of, 1426; *see also under* Optic, Visual, &c.
Eyeball, nerves of, 1288; compression of, 1371; movements of, 1388, 1394–1398; muscles of, 1398–1402; co-ordination, 1402
Eyelashes, follicles of, 1428
Eyelids, structure of, 1426; droop of, 1426; animals with three, 1427

Facial nerve, *see* Seventh
Fallopian canal, position of, 1439
Fatigue, its connection with the muscular sense, 1557
Feeble illumination, the fovea insensitive to, 1333; visual purple important in the perception of, 1370
Fenestra ovalis, position of, 1434, 1438; attachment of stapes to, 1447; transmission of auditory vibrations by, 1447, 1487
Fenestra rotunda, position of, 1434, 1438; action of auditory vibrations on, 1447, 1487
Fenestrated layer (membrane), *see* Molecular layers
Fibres of ciliary muscle, action of, in accommodation, 1286; of optic nerve, 1306; of retina for primary sensations, 1345; of basilar membrane, of, 1476; *see also under* Optic, Pupil-constrictor, Radial, &c
Fibrinogen, in aqueous humour, 1422
Field of sight, defined, 1389; difference between field of vision and, 1410
Field of touch, 1531, 1533
Field of vision, defined, 1376, 1389; binocular, 1390; general features

of, 1409; difference between field of sight and, 1410; struggle of the two fields, 1418
Fifth nerve, ophthalmic division of, 1289; branches of, stimulation, cause of tears, 1428; control of the tensor tympani, 1449, 1450; its connection with the olfactory mucous membrane, 1501, 1503; effect of injury, 1507; connection with the organs of taste, 1508, 1515, 1520, 1521, 1546; its junctions with the seventh and glossopharyngeal, 1520
Filiform papillæ, *see* Papillæ
First visceral cleft, *see* Hyomandibular
Fishes, mechanism of accommodation in, 1286; constriction of pupil in, 1295; visual purple in rods of, 1369; no cochlea, 1495
Fixation point of vision, 1388
Flavours, 1513
Flicker photometry, 1360
Flickering, the phenomenon of, 1327; influence of contrast on, 1384
Fluorescence of media of eye, 1305
Fluorescin, injection of, effect on aqueous humour, 1423
Focus, principal anterior, 1259, 1262; principal posterior, 1259, 1262; of emmetropic eye, 1298
Fog, effect on visual judgment, 1415
Follicles of eyelashes, 1428
Fontana, *see* Spaces of
Foramina nervina, position and structure of, 1473
Fornix conjunctival, 1427
Fourth nerve, control of superior oblique muscle by, 1402
Fovea centralis, position of, 1260, 1307; structure of, 1317; effect of luminous stimulation, 1331–1333; insensitive to feeble light, 1333; sensational units in, 1333; blindness of, in total colour-blindness, 1371
Frog, constriction of pupil in, 1295
Fundamental tone of the membrana tympani, 1445, 1478
Fungiform papillæ, *see* Papillæ
Fuscin, occurrence in pigment epithelium of retina, 1320, 1368

Galton's whistle, 1479
Gamboge, absorption of blue rays by, 1337; mixed with indigo, 1338
Ganglion spirale, position and structure of, 1459, 1473; *see also* Lenticular, Ophthalmic, &c.
Ganglionic cells, layer of, 1307, 1315; of macula lutea, 1317
General sensibility, *see* Common sensibility
Ghost, idea of, 1561
Glands of Bowman, 1502
Glands of eye, 1428
Glands of membrane of mouth, 1509, 1511, 1515
Glans penis, sensitive to heat, 1548
Globules of cones, 1374
Globulin in the lens, 1281; in vitreous humour, 1281; in aqueous humour, 1422
Glossopharyngeal nerve, its connection with the organs of taste, 1508, 1511, 1515, 1520, 1546; junctions with the fifth and seventh nerves, 1520
Goblet cells of nasal mucous membrane, 1501
Gold chloride, treatment of epithelium with, 1527, 1528
Golgi, *see* Organ of
Grandry's corpuscles, structure and distribution of, 1525
Granular layers of retina, *see* Nuclear
Green, wave-lengths of, 1339, 1342; wave-length of unchanging, 1352; confusion in colour-blindness, 1353, *et seq.*
Green blindness, 1354, 1356
Grey, production of, 1340; neutral, 1350
Gustatory sensations, 1513–1521; enumeration of, 1513, 1514; most favourable temperature for, 1515; contrast of, 1516; distribution of, 1517; possible connection with chorda tympani, 1520
Gymnema sylvestre, its action on the gustatory organs, 1518

Haidinger's brushes, 1305
Hair-cells, inner and outer, of rods of Corti, 1468; structure of inner, 1471; of outer, 1472; number of, 1476; *see also* Cylinder cells
Hair follicles and touch points, 1551
Hallucinations, visual, 1387; auditory, 1496
Hammer bone, *see* Malleus
Hamulus, position of, 1458
Handle, *see* Manubrium
Harderian gland, 1428
Hearing, 1430, *et seq.*
Heat, *see* Sensations of heat and cold
Heat points, 1535, 1548
Helicotrema, position of, 1458
Helmholtz, his phakoscope described, 1271; his primary colour theory, *see* Young-Helmholtz theory
Hemianopia, 1291, 1330
Hemiopic pupil reflex, 1291
Hensen's body, 1472
Hensen's cells, 1468
Herbst's corpuscles, structure of, 1523
Hering, his theory of primary-sensations, 1345–1348; compared with the Young-Helmholtz theory, 1350, 1385; his four primary colours, 1352; colour-blindness explained by, 1354, *et seq.*;

explanation of negative images, 1382; simultaneous contrast explained by, 1385
Heteronymous diplopia, 1393
Homonymous diplopia, 1393
Horizon, visual judgment of objects on, 1416
Horizontal cells, of retinal layers, 1314
Horopter described, 1407
Hue of colours defined, 1340, 1341; of red of spectrum, 1351, 1355
Hunger, sensations of, 1541–1543
Hyaloid canal, 1424
Hyaloid membrane, 1281
Hydrocyanic acid, odourless to some individuals, 1505
Hyomandibular visceral cleft, position of, 1433
Hypermetropia, causes of, 1298
Hypermetropic eye, limits of accommodation for, 1269; ciliary muscles of, 1286; spectacles for, 1298

Idea, an, defined, 1387
Identical points, *see* Corresponding
Illusions, visual, 1411; *see* Hallucinations
Image, *see* After, Mental, Retinal
Impulses, *see* Auditory, Gustatory, Visual, &c., &c.
Incus, 1434, 1438; teeth of, 1442; ligament of, 1442; part of a lever, 1443
Indigo, absorption of red and yellow by, 1337; mixed with gamboge, 1338; wave-length of, 1342
Indirect vision, 1407
Intensity of colours defined, 1340
Internal ear, *see* Ear
Intraepithelial fibrillæ, 1528
Intraepithelial plexus, 1527
Intraocular tension, 1421; pressure, 1425
Intrinsic light of retina, 1349
Iridescence of surface of choroid, 1275
Iridic angle, 1278, 1423
Iris, structure of, 1256, 1276, 1277; pigment of, 1276; muscular fibres of, 1276, 1287; blood vessels of, 1419
Irradiation, 1379
Irregular astigmatism, 1301

Joints, movements of, connected with muscular sense, 1557

Katabolic phase, in metabolism, 1346, 1382; Hering's term for, 1348

Labium tympanicum, *see* Tympanic lip
Labium vestibulare, *see* Vestibular lip
Labyrinth, *see* Bony, Membranous, *and* Vestibular labyrinth
Lachrymal canaliculi, 1428
Lachrymal gland, 1428
Lachrymal sac, 1428
Lamina, anterior elastic, *see* Membrane of Bowman; posterior elastic, *see* Membrane of Descemet
Lamina cribrosa of sclerotic coat, 1273, 1306
Lamina fusca, 1274
Lamina spiralis, position of, 1458
Layers of retina, 1307, 1374; *see also* Corneous, Nuclear, &c., &c.
Lens, development of, 1256; refractive powers of different parts, 1260; surfaces of, 1260; mean refractive index of, 1261; measurement from anterior surface of, to anterior surface of cornea, 1261; measurement of radius of anterior and posterior surfaces of, 1261, 1262; measurement of thickness of, 1261; curvature of anterior surface, in accommodation, 1270, 1283–1287; radius of curvature for near vision, 1271; accommodation lost by removal of, 1272; development and structure of, 1280; imperfections in, 1303; nutrition of, 1420
Lenticular ganglion, 1288
Leucocytes, in the chorio-capillary membrane of myopic eyes, 1274; in vitreous humour, 1281
Levator palpebræ superioris, 1426
Ligaments, of the ossicles, 1441, 1442; of incus, 1442; afferent nerves of, 1557
Ligamentum pectinatum, 1279
Ligamentum spirale, *see* Spiral ligament
Light, sensation of, defined, 1253; paths of rays to retina, 1260, 1262; difference of brightness just appreciable, 1325; transformation of energy of, 1363; nature of, 1366; as a stimulus to living matter, 1367; *see also under* Visual sensations, Impulses, &c.
Limbus, of cochlea, position and structure of, 1464
Limiting membranes of the retina, position of, 1308; structure of inner, 1309
Limits of audible vibrations, 1479, *et seq*
Line of fixation, 1388
Line of vision, *see* Visual axis
Lines of separation defined, 1393
Lips, effect of movements of tongue and, 1515; "smacking" the lips, 1515
Listing, schematic eye of, 1261, 1262
Listing's law, 1395
Living matter, light as a stimulus to, 1367
Localization of auditory sensations, 1497
Locomotor ataxy, *see* Tabes dorsalis
Long process of incus, position of, 1436; ligament of, 1442

Long root, of ciliary ganglion, 1288
Long-sighted eye, *see* Hypermetropic eye
Longitudinal bundle, posterior, fibres of, 1407
Longitudinal sound-waves, 1445
Loudness, defined, 1477; distinction of, 1481, 1494
Luminous points, angle of fusion for two, 1332
Luminous rays, compared with thermic rays, 1367
Luminous undulations of colour sensations, 1336
Lustre defined, 1418
Lymph, in cornea, flow of, 1278
Lymphatics of eye, 1420–1425; mechanical functions of, 1421

Macula acustica, position and structure of, 1455, 1463; function of, 1488
Macula lutea, position of, 1307; structure of, 1317; colour of, 1318; luminous stimulation of, 1331, 1332; sensational units of, 1333; influence on colour sensations, 1352
Magic lantern, illustration of visual judgment, in pictures of, 1415
Malleus, position of, 1434, 1438; structure of, 1435; teeth of, 1442; part of a lever, 1443
Malpighian layer, nerve endings in, 1528
Manubrium, position of, 1435
Mastoid bone, air cells of, 1438
Maxwell, his primary colour theory, *see* Young-Helmholtz theory
Meatus auditorius
  internus, position of, 1433, 1455
  externus, position of, 1434; passage of sounds by, 1447
Median plane of vision, 1389
Meibomian glands, 1428
Membrana capsulo-pupillaris, formation of, 1257, 1258
Membrana flaccida, position of, 1439
Membrana pupillaris, formation of, 1257
Membrana reticulata, *see* Reticulate membrane
Membrana tectoria, *see* Tectorial membrane
Membrana tympani, position of, 1433, 1436; structure of, 1439; transmission of sound by, 1444, *et seq.*; action of aerial sound-waves on, 1445; fundamental tone of, 1446; ‘damped,’ 1446; vibration of a dead, 1490
Membrane of Bowman, position of, 1278
Membrane of Bruch, 1274, 1275, 1277, 1307
Membrane of Descemet, position of, 1278, 1279
Membrane of the mouth, 1508–1512; action of acid on, 1513
Membrane of Reissner, position and structure of, 1459, 1465
Membranes, *see also under* Basal, Basilar, Buccal, Limiting, Mucous, &c., &c.
Membranous canal, 1455
Membranous labyrinth, position of, 1433; structure of, 1452–1460; action of auditory vibrations on, 1487
Mental image, compared with retinal image, 1378
Meridional ciliary muscle, *see* Ciliary muscle, longitudinal
Mesoblast, of choroidal fissure, 1254
Mesoblastic tissue of otic vesicle, changes in, 1431
Metallic tastes, 1514
Modiolus of cochlea, 1456
Molecular layers of retina, 1307, 1313
Monocular visual judgments, 1414
Motor nervous impulses, coordination of, 1402, 1404
Mouth, the membrane of, 1508; distribution of sensitiveness of, 1516
Movement, sense of, 1553
Movements of tongue and lips, effect of, 1515
Mucin, in perilymph of vestibular labyrinth, 1460; in endolymph, 1464
Mucous glands of conjunctiva, 1428
Mucous membrane of conjunctiva, 1427; of the tympanum, 1441; of Eustachian tube, 1450; of the mouth, *see* Membrane of the mouth
Müller, muscle of, *see* Ciliary muscle, Circular muscle
Müller, radial fibres of, 1308
Muscæ volitantes, 1303
Muscles, *see* Ciliary, Dilator, &c.
Muscle of Müller, *see* Ciliary muscle, Circular muscle
Muscles of eyeball, *see* Ocular muscles
Muscle spindles, 1557
Muscular fibres of tongue, 1509
Muscular sense, 1552–1558; and cutaneous sensations, 1555, 1559
Musculi obliqui, the actions of, 1398; nervous control of, 1402
Musculi recti, the actions of, 1398; nervous control of, 1402; connection of the, with eyelids, 1427
‘Musical ear,’ the sensitiveness of a, 1480, 1494
Musical sounds defined, 1477
Myopia, causes of, 1298
Myopic eye, limits of accommodation for, 1268, 1269; the chorio-capillary membrane of, 1274; ciliary muscle of, 1286; spectacles for, 1298

Nasal mucous membrane, *see* Olfactory
Nasal catarrh, effect on sense of smell, 1504
Nausea, sensation of, 1543

Negative image, *see* After image
Nerves, *see under* Auditory, Glossopharyngeal, Optic, &c., &c.
Nerve endings of skin, 1522–1528; stimulation of, 1546; for sensations of pressure, of heat, and of cold, 1547
Nervous elements of retina, 1310
Nervous mechanism of accommodation, 1295–1297
Nervus abducens, *see* Sixth nerve
Nervus trochlearis, *see* Fourth nerve
Neuroglia, of optic nerve, 1306; of the limiting membranes, 1309
Neuroglial elements of retina, 1308
Neurokeratin, formation of, 1309
Neutral band in colour-blindness, 1353
Neutral grey, *see* Grey
Nicol's prism, entoptic phenomena in use of, 1305
Nocturnal animals, visual purple in rods of, 1369
Nodal point of optical system, 1259, 1262
Noises defined, 1477
Note defined, 1478
Nuclear layers of retina, 1307, 1313, 1462
Nutrition of eye, 1419–1425

Oblique muscle, superior and inferior, actions of, 1398, 1399
Occipital cortex, action of visual impulses on, 1377, 1405; stimulation of, 1405
Ocular muscles, 1398–1402; respective functions of, 1399; enumeration of, 1401; nervous control of, 1402
Ocular phantoms, 1387
Oculo-motor nucleus, 1291
Œsophagus, tactile sensations in, 1536
Olfactometer, use of, 1506
Olfactory epithelium, structure of, 1501
Olfactory lobes, effect of loss of, 1507
Olfactory mucous membrane, structure of, 1501–1503; moistening fluid of, 1504; chemical stimulation of, 1505
Olfactory nerve, 1501; fibres of, 1503; disputed function of, 1507
Olfactory sensations, 1504–1507; defects, 1505; oscillation of, 1506; neutralization of, 1506; localization of, 1507; reflex effects, 1507; in lower animals, 1507
Opening of the eye, mechanism for, 1426
Ophthalmic ganglion, 1288
Ophthalmoscope, described, 1373; methods of use, 1374
Optic axis, position of, 1259–1260
Optic cup, *see* Retinal cup
Optic disc, position of, 1307, 1424
Optic fibres, layer of, 1307; structure of, 1315
Optic nerve, early development of, 1255; fibres of, 1256; position and structure of, 1256, 1306; action of, in constriction of pupil, 1290; in dilation of pupil, 1294; atrophy of, 1296; connection with rods and cones, 1308; effect of division and stimulation of, 1329; lymph-spaces of, 1421, 1424
Optic oculo-motor mechanism of pupil, 1294
Optic papilla, *see* Optic disc
Optic vesicle, development and structure of, 1254
Optical phenomena, their close connection with electrical, 1366
Optical system, description of, 1259; simplification of, 1261
Optogram, method of obtaining, 1369
Ora serrata, position of, 1257; connection of fibres of Müller with, 1309
Orange, production of the colour, 1338; wave-length of, 1342
Orbicularis oculi, 1426; paralysis of, effect on path of tears, 1429
Organ of Corti, position of, 1459, 1467; structure of, in different mammals, 1475, 1476; length in man, 1476; functions of, 1489
Organ of Golgi, 1557
Os orbiculare (lenticulare), position of, 1436
Ossicles, *see* Auditory
Otic vesicle, position and structure of, 1431
Otoconia, position of, 1464; functions of, 1494
Otoliths, position of, 1464; functions of, 1489, 1494
Over-tones, 1478
Owl, visual purple in rods of, 1369

Pacinian corpuscles, localities for, 1522, 1524; structure of, 1523; functions of, 1551, 1558
Pain, *see* Sensations of
Papillæ of the tongue, 1509; sensitiveness of fungiform, 1517
Papillæ foliatæ, 1509, 1510
Papilla, optic, *see* Optic disc
Paradoxical sensations, 1548
Pars ciliaris retinæ, position of, 1257, 1276; secretory activity, 1423
Partial tones, 1478
Passages of ear, *see* Auditory passages
Pathetic muscle, *see* Oblique muscle
Pencil of rays of light, formation of, 1262
Perception, *see under* Visual, &c.
Perichoroidal space, position of, 1273
Perilymph of tympanic cavity, composition of, 1460; vibrations of, 1487
Periodic law, 1505
Peripheral part of retina, effect of colour sensations on, 1351, 1357
Peripheral process, 1314, *see* Dendrite
Perivascular lymph-spaces, 1421

Petit, *see* Canal of
Phakoscope, description of, 1271
Phalangæ, 1470
Phalangar process, 1470, 1472
Phantoms, see Auditory, Ocular, Tactile, &c.
Pharynx, tactile sensations in, 1536
Phonogram, the production of a, 1490
Phosphenes, sensation of, 1328
Photerytherous class of colour-blindness, 1354, 1357
Photochemistry of retina, 1367–1375
Photophobia, 1371
Physostigmin, effect of, on pupil, 1295, 1296
Pia mater, connection with optic nerve, 1306
Pial sheath of optic nerve, 1306, 1424
Pig's snout, epidermis of, 1528
Pigment, in corpuscles of sclerotic coat, 1273; of choroid, 1275; of ciliary processes, 1275; of iris, 1276; of macula lutea, 1318; colour sensations influenced by pigment of macula lutea, 1352
Pigment-epithelium of retina, 1256; 1275, 1307; structure of, 1319; changes on action of light, 1320, 1368
Pinna, 1434
Pitch, defined, 1478; distinction of, 1480
Planes, principal, of eye, 1261
Position, sense of, 1553
Posterior canal, *see under* Semicircular
Presbyopia, causes of, 1298
Presbyopic eye, limits of accommodation for, 1269; spectacles for, 1299
Pressure, sensations of, *see* Tactile sensations
Pressure points, 1531, 1550; hair follicles and, 1551
Primary colour sensations, 1341; curves of, 1344; *see under* Young-Helmholtz, *and* Hering
Primary olfactory sensations, 1506
Primary position of eyeballs, 1394
Primary visual centres, action of visual impulses on, 1377; their connection with the co-ordinated ocular movements, 1405, 1406
Principal anterior and posterior focus, *see* Focus
Principal points of optical system, 1259, 1261, 1262
Principal ray, *see under* Rays of light
Prism, *see* Spectrum, *and* Nicol's prism
Process, *see* Ciliary, Long, Short, &c.
Processus brevis, position of, 1435
Processus gracilis (Folianus), position of, 1435
Promontorium, position of, 1459
Protective mechanism of the eye, 1426–1429
Proteids in the lens, 1281; in vitreous humour, 1281; in aqueous humour, 1422; in tears, 1428
Punctum lachrymale, 1428
Pungent tastes, 1516, 1519
Pupil, position of, 1257; structure of, 1257; contraction of, for near accommodation, 1270, 1286; movements in accommodation, 1287–1297; mechanism of, 1287; constriction of, a reflex act, 1290; co-ordination in movements, 1291; change in margin of, 1302
Pupil-constrictor fibres, 1291
Pupil-dilator impulses, mode of action of, 1293
Purkinjé's figures, 1363
Purple, production of, 1339
Purple, visual, 1310, 1368, *et seq.*; function of, 1370; electrical phenomena independent of, 1375

Quality of sound defined, 1478
Quinine, its taste, 1514

Rabbit, the taste-buds of, 1509
Radial fibres of Müller, 1308
Radiate muscle of iris, 1276
Rami perforantes, 1527
Ray of light, paths of, to retina, 1260, 1262; formation of pencil of, 1262; principal ray, 1263
Reaction period, in visual sensations, 1326
Rectum, tactile sensations in, 1536
Rectus muscle, *see* Musculi recti
Recurrent auditory sensations, 1497
Recurrent image, 1381
Red, wave-lengths of, 1336, 1342, 1351; wave-length of unchanging, 1352; confusion in colour-blindness, 1353, *et seq.*; by evening light, 1360, 1370
Red blindness, 1354, 1355
Red-green blindness, 1353, *et seq.*
Reflex effects of olfactory sensations, 1507
Reissner, *see* Membrane of
Renal colic, 1538
Reptiles, mechanism of accommodation in, 1286; cones of eye in, 1374; cochlea of, 1476
Respiratory mucous membrane of nose, 1501
Reticular layers, *see* Molecular
Reticulate membrane, 1470
Retina, functions of, 1254; early development of, 1255; layers of, 1307; a portion of the brain, 1308; supporting elements, 1308; nervous elements, 1310; disposition of rods and cones, 1312, 1313; blood vessels, 1318;

adaptation of, in dark, 1323; electrical stimulation of, 1328, 1375, 1386; mechanical stimulation of, 1328, 1385; visual areas of, 1333; colour vision of periphery of, 1351; chemical changes, in, 1366; effect of vibrations of ether on, 1366; photo-chemistry of, 1367–1375; treatment of removed, for optogram, 1369; result of exhaustion of, 1381; corresponding parts of, 1407
Retinal cup, development of, 1255
Retinal currents, 1375
Retinal image, formation of, 1258–1264; inversion of, 1264, 1305, 1330; observation of images reflected from the eye, 1271; position of, 1328; compared with mental image, 1378
Rod bipolar cells, *see* Bipolar cells
Rod cells, of auditory epithelium, 1463; of olfactory mucous membrane, 1502; of taste-buds, 1510
Rod fibre, 1312
Rods and cones, position of layer of, 1307; connection with optic nerve, 1308; structure of, 1310–1313; inner and outer limbs, 1310; structure of rod and of cone, 1312; disposition of, over the retina, 1312, 1313; functions of the rods, 1368, *et seq.*; reflection of rays of light by, 1373; difference between rods and cones, 1374
Rods of Corti, structure and position of, 1467; inner and outer, 1469; fluid of tunnel of, 1474; absent in birds and reptiles, 1476; number of, 1476; theories of action of, 1491
Rotation, centre of, in eyeball, 1388

Saccharine, taste of, 1518
Saccule, position of, 1431, 1438, 1453; structure of, 1454; function of, 1494
Saccus endolymphaticus, 1454
Salamander, constriction of pupil in, 1295
Salt tastes, 1517
Santonin, production of violet blindness by, 1358
Sapid substances, gustatory sensations of, 1514
Sarcolactic acid, in aqueous humour, 1422
Saturation of colours, 1340; in Hering's theory, 1349
Scala media, position of, 1458
Scala tympani, position of, 1458
Scala vestibuli, position of, 1458
Scheiner's experiment, 1266
Schematic eye of Listing, 1261, 1262
Schlemm, *see* Canal of
Schneiderian membrane, *see* Respiratory mucous membrane
Sclerotic coat, of eye, 1256; structure of, 1273; pigment of, 1273; connection with optic nerve, 1306; blood vessels of, 1420; lymph-spaces, 1421
Scoterytherous colour-blindness, 1354, 1357
Seat of consciousness, 1549
Sebaceous glands of follicles of eyelashes, 1428
Sensations, *see under* Auditory, Cutaneous, Visual, &c.
Sensations of heat and cold, 1533–1536; contrast in, 1535; localization, 1535; other localities for, than the skin, 1536; terminal organs for, 1547
Sensations of pain, 1537–1543; analysis of, 1537; localization and distinction, 1538, 1539
Sensations of pressure, *see* Tactile sensations
Sensations of temperature, *see* Sensations of heat and cold
Sensations of touch, *see* Tactile sensations
Semicircular canals, position of, 1431, 1433, 1439, 1454
Serum albumin, in aqueous humour, 1422
Seventh (facial) nerve, connection with mechanism of eye, 1426; connection with the tympanum, 1439; control of the stapedius, 1450; its junctions with the fifth and glossopharyngeal nerves, 1520
Short process of incus, position of, 1436
Short root of ciliary ganglia, 1288
Short-sighted eye, *see* Myopic eye
Shutting of the eye, mechanism for, 1426
Sight, 1253, *et seq.*
Sight and touch, connection between, 1560
Simultaneous contrast, in vision, 1379; influence on flicker, 1384; in taste, 1516
Singing in the ears, cause of, 1496
Sixth nerve, its control of the external rectus, 1402
Size, visual appreciation of apparent, 1412; perception of actual, 1413, 1415
Skin, afferent nerves of, 1522; nerve-endings of, 1527; varying sensitiveness of different parts, 1530, 1532, 1535; painful sensations in, 1537, 1540
Skull, transmission of sound through, 1448
'Sleep,' the sensation of an arm or leg 'gone to sleep,' 1548
Smell, 1501, *et seq.*; confusion of sensations of taste and, 1513; sensations of, *see* Olfactory sensations

Snakes, mechanism of accommodation in, 1286

Sodium chloride, in aqueous humour, 1422; in tears, 1428

Solidity in vision, perception of, 1408, 1412, 1416–1418

Sound, conduction of, through the tympanum, 1444–1451; through the skull, 1448; on auditory sensations, 1477–1486; distinction of, 1480; the transmission of complex auditory vibrations, 1489; appreciation of, 1494; localization, 1497; judgment of direction, 1498; judgment of distance, 1499; *see* Auditory impulse, &c.

Spaces of Fontana, 1279, 1423, 1424

Spectacles, for various sights, 1298

Specific energy of nerves, theory of, applied to cutaneous sensations, 1545

Spectrum, in chromatic aberration, 1301; the series of colour sensations from, 1337; as seen by the colour-blind, 1353; colourless, of dark-adapted eye, 1360, 1370

Spherical aberration, 1299

Sphincter iridis, *see* Sphincter muscle

Sphincter muscle of iris, 1276; action of, in accommodation, 1287; compared with the heart, 1293

Spindles, *see* Muscle spindles

Spiral groove, position of, 1465

Spiral ligament, position of, 1465

Spiral strands, inner and outer, of cochlear nerve, 1474

Spongioblasts, *see* Amacrine cells

Squinting, 1403

Stalk, solid, of retinal cup, 1255

Stapedius muscle, 1448; position, structure and functions of, 1450; effect of paralysis of, 1480

Stapes, position of, 1434, 1438; foot of, 1442, 1447; part of a lever, 1443

Stereoscope, limitation of ocular movements illustrated by, 1403

Stimulation, of retina, ratio of the stimulus to the sensation, 1324; effect of duration of stimulus, 1325, 1326; duration of intervals between stimuli, 1327; mechanical stimulation of retina, 1328, 1385; of the gustatory organs, 1514, 1519; of chorda tympani, 1520; of limbs, effect on muscular sense, 1558; *see also* Electrical stimulation, Visual sensations

Stimulus, *see under* Stimulation

Stirrup bone, *see* Stapes

Stratum granulosum, 1528

Stria vascularis, *see* Vascular band

Subarachnoid space, 1424

Sub-basal plexus, 1527

Subepithelial plexus, 1527

Subsidiary auditory apparatus, structure and functions of, 1430–1451

Subsidiary cells of taste-buds, 1510

Successive contrast, in vision, 1382; in taste, 1516

Sulcus spiralis, *see* Spiral groove

Summation tones, 1485

Superior canal, *see under* Semicircular

Supporting elements of retina, 1308

Suprachoroidal membrane, 1274

Supravaginal cavity, position of, 1421

Suspensory ligament of eye, formation of, 1258; structure and connections, 1281, 1282; action of, in accommodation, 1283

Swallowing, effect on the Eustachian tube, 1451

Sweet tastes, 1514, 1517

Sympathetic mechanism of pupil, 1294

Sympathetic root of ciliary ganglion, 1289

Synapsis, 1313–1316

Tabes dorsalis, effect of the disease on cutaneous sensations, 1547; on muscular sense, 1555

Tactile illusions, 1562

Tactile judgment, 1559–1562

Tactile perception, 1531, 1559–1562

Tactile phantoms, 1562

Tactile sensations, 1529–1533; fusion of, 1530; localization of, 1531; other localities for, than the skin, 1536; terminal organs for, 1547; muscular sense and, 1555, 1559; visual sensations associated with, 1560

Tapetum in carnivora, structure of, 1275

Tarsus of eyelids, 1426

Taste, structure of organs of, 1508–1512; sensations of, *see* Gustatory sensations; confusion of sensations of smell and, 1513; specific terminal organs for, 1518; possible connection with chordi tympani, 1520

Taste-buds, structure of, 1509

Taste-bulbs, *see* Taste-buds

Tears, composition and causes of, 1428, 1429

Tectorial membrane, position of, 1465; structure of, 1475

Temperature, *see* Sensations of heat and cold

Tendons, afferent nerves of, 1557

Tenon's capsule, position of, 1273; structure of, 1421

Tenonian cavity, position of, 1421

Tension, intraocular, 1421

Tensor tympani muscle, position of, 1435; description of, 1448; functions of, 1449; crackling noise produced by, 1450

Thermic rays, compared with luminous rays, 1367

Third (oculo-motor) nerve, position of, 1288, 1289: action of, in constriction

of pupil, 1290; in dilation of pupil, 1294; control of the ocular muscles by, 1402, 1426
Thirst, sensations of, 1541–1543
Tickling, the sensation of, 1543
Timbre, *see* Quality
Tint of colours defined, 1341
Tissue, *see* Mesoblastic, &c.
Tone defined, 1478
Tones, *see* Fundamental, *and* Partial
Tone of colours defined, 1341
Tongue, structure of, 1509, 1519; electric stimulation of, 1513; movements of, 1515
Touch and sight, connection between, 1560
Touch-cells, 1528
Touch-corpuscles, localities for, 1522, 1526; structure of, 1525
Touch-points, *see* Pressure points
Transversal sound-waves, 1445
Trichromic vision, 1343, 1350
Trochlea, 1398
Trochlear muscle, *see* Oblique
Tunica propria, 1460
Tuning-fork, vibrations of, 1445
Tunnel of organ of Corti, 1467, 1468; spiral strand of, 1474; fluid of, 1474
Turgescence, vascular, effect on pupil, 1288
Tympanic cavity, position of, 1434, 1459
Tympanic lip, position of, 1465
Tympanic membrane, *see* Membrana tympani
Tympanum, conducting apparatus of, 1435–1444; structure of, 1436; conduction of sound through, 1444–1451; muscles of, 1448; influence on auditory sensations, 1480

Ulnar nerve affected by dipping elbow into a freezing mixture, 1546
Umbo, position and structure of, 1440
Undulation, *see* Luminous
Urea in aqueous humour, 1422
Utricle, position of, 1431, 1438, 1453; structure of, 1454; function of, 1494

Vagus nerve, effect of division, 1542
Vas spirale, position and functions of, 1467
Vascular band of canalis cochlearis, 1466
Vaso-motor nerves of the eye, 1420
Vena centralis, 1419
Venæ vorticosæ of choroid, 1274, 1419
Venous congestion of head, cause of flow of tears, 1428
Venous plexuses of membrane of mouth, 1511
Ventriloquism, 1500
Vesicle, *see* Optic
Vestibular labyrinth, structure of, 1460–1464; effect of injury of, 1494; in fishes, 1495
Vestibular lip, position of, 1465
Vestibular nerve, composition of, 1455; its functions other than auditory, 1494; connection with coordination of movement, 1553
Vestibule, position of, 1433
Vibrations, auditory, *see* Sound-waves
Violet, wave-length of, 1336, 1342, 1351; as a primary colour, 1351; in colour-blindness, 1358, *et seq.*
Violet blindness, 1358
Vision, physiological and psychological elements in the study of, 1376; double, 1403; indirect, 1407; region of distinct, 1331, 1332; trichromic, 1343, 1350; *see also under* Binocular, Optic, Sight, Visual
Visual acuity, test of, 1330; normal, 1333; low, of total colour-blindness, 1371
Visual angle, minimum, defined, 1330
Visual areas of retina, 1333
Visual axis, 1388; co-ordination of axes, 1403
Visual effect of luminous points, 1323
Visual field, *see* Field of vision
Visual impulses, defined, 1253, 1322; development of, 1362–1375; origin of, 1366; action of, on brain, 1377
Visual judgments, 1411–1418; in monocular vision, 1414
Visual perceptions, 1376–1387; false, 1387; some features of, 1409–1418
Visual plane, 1389
Visual purple, white, yellow, *see* Purple, White, Yellow
Visual sensation, defined 1264; some general features of, 1323–1335; ratio of the stimulus to, 1324; curve of, 1325; duration of, 1325; fusion of, 1327; produced by other agents than light, 1328, 1385; size and, 1331; the sensational unit, 1333; differentiation of, by the brain, 1334; metabolism and, 1346; developed in brain, 1372; some features of, 1376–1387; co-ordination of, 1376; association of, with tactile sensations, 1560; *see also* Colour sensations
Visual substance, 1346; argument for, 1371, 1372
Vitreous humour, development of, 1256; refractive powers, 1260, 1261; analysis of, 1281; after death, 1282; reflection of rays into, 1373; nutritive supply of, 1420, 1421; description of, 1424, 1425
Volitional impulses, action of, 1405

Water, accommodation of eye under, 1270; action on olfactory mucous membrane, 1504

Waves of sound, action of, on auditory apparatus, 1430, 1434, 1487; paths of, 1435; conduction through the tympanum, 1444–1451; aerial, 1445; transmitted through the skull, 1448; the nature of, 1478, *et seq.*; compounded, 1483; a curve of, 1490
Wave-lengths of various colours, a list of, 1342
Wax of ear, 'singing' caused by, 1496
Weber's law of visual sensations, 1325; as applied to auditory sensations, 1480; as applied to tactile sensations, 1530, 1535
Whisker of cat, touch-cells in, 1528
'White,' the sensation of, 1336; combination of colour with, 1340; production of, by mixture of two colours, 1341; production of, by mixture of three colours, 1342; its nature in the two theories of colour vision, 1349; visual, 1369
Whorls of cochlea, position of, 1438, 1456; measurements of, 1476
Winking, mechanism of, 1426

Yellow, wave-lengths of, 1342; wave-length of, unchanging, 1352; in colour-blindness, 1357, *et seq.*; by evening light, 1360, 1370; visual, 1369
Yellow-blue blindness, 1358
Yellow spot, *see* Macula lutea
Young-Helmholtz colour theory, 1343–1345; compared with the Hering theory, 1350, 1385; colour-blindness explained by, 1354, *et seq.*; Donders' modification of, 1372; negative images explained by, 1382; simultaneous contrast explained by, 1384

Zenith, visual judgment of objects at the, 1416
Zonule of Zinn, 1282, 1425

## ERRATA.

p. 1274, l. 44, *for* 'myoptic' *read* 'myopic.'
p. 1323, l. 37, *for* 'homononymous' *read* 'homonymous.'

CAMBRIDGE: PRINTED BY J. AND C. F. CLAY, AT THE UNIVERSITY PRESS.